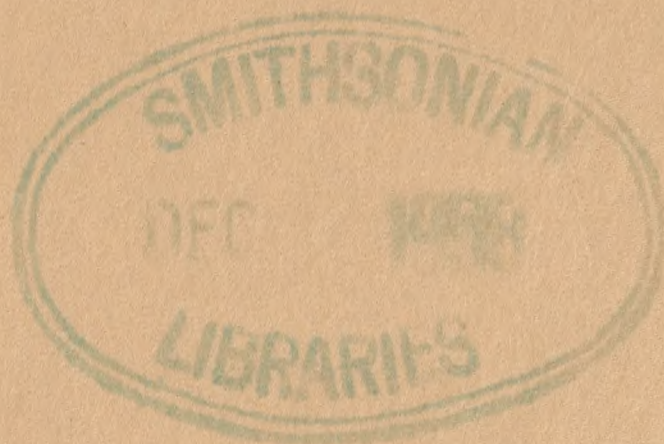






*Contributions
of the
American Entomological Institute*

Volume 4, Number 1, 1968



MOSQUITO STUDIES (Diptera, Culicidae)

X. Dixinae originally described from North America.

By

By T. Michael Peters

XI. Mosquitoes originally described from Argentina,
Bolivia, Chile, Paraguay, Peru, and Uruguay.

By

John N. Belkin, Robert X. Schick, and Sandra J. Heinemann

CONTRIBUTIONS
of the
AMERICAN ENTOMOLOGICAL INSTITUTE

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- No. 1. Mosquito studies (Diptera, Culicidae), 1968.
- X. Peters, T. Michael. Dixinae originally described from North America. 7 pages.
- XI. Belkin, John N., Robert X. Schick, and Sandra J. Heinemann. Mosquitoes originally described from Argentina, Bolivia, Chile, Paraguay, Peru, and Uruguay. 29 pages. Price of X and XI: \$1.25, postpaid

MOSQUITO STUDIES (Diptera, Culicidae)

X. DIXINAE ORIGINALLY DESCRIBED FROM

NORTH AMERICA¹

By

T. Michael Peters²

Belkin, Schick and Heinemann (1966) presented all the available data on the source of the type material for all the nominal species of Culicinae and Chaoborinae originally described from North America north of Mexico. In the present paper the treatment of the family Culicidae in the broad sense is completed for North America by similar information for the Dixinae. The data are presented in the same manner. Included in the list are species described by Peters in Peters and Cook (1966), whose taxonomic treatment is followed here.

LIST OF SPECIES

Dixinae

The habitats of the immature stages of the Dixinae have been recorded for only 16 species in North America. This information is given below under BIONOMICS for each of these species. For all the other species the following information is presented here as a guide to locating breeding sites. In general the larvae and pupae are found among vegetation or debris along the margins of various bodies of ground water. They are particularly abundant on the margins of very small streams, springs or seepages but occur also in pools in larger, swifter streams as well as in permanent, semipermanent and temporary stagnant pools, ponds, lakes and even in bogs and swamps. Occasionally they may be present in artificial containers.

256. Dixa arge Dyar & Shannon, 1924b:199-200. TYPE: Holotype ♂, Longmire Springs (Mt. Rainier National Park), Washington, 14 June 1917, H. G. Dyar (USNM, 27454). BIONOMICS: [Larvae probably among emergent vegetation in clear, eurythermous, moderately fast, acidic to neutral, shallow streams or small rivers.]

¹Contribution from project "Mosquitoes of Middle America" supported by Public Health Service Research Grant AI-04379 and U. S. Army Medical Research and Development Command Research Contract DA-49-193-MD-2478.

²Department of Entomology, University of Massachusetts, Amherst, Mass. 01002.

257. *Dixa blax* Dyar & Shannon, 1924b:199. TYPE: Holotype ♂, Bright Angel (Coconino Co.), Arizona, 10 May 1903, H.S. Barber (USNM, 27453).

258. *Dixa brevis* Garrett, 1924a:6. TYPE: Holotype ♂, McLean Creek, about 2 mi from mouth, Okanagan Falls, British Columbia, 23 Sept, C. Garrett (CNC). BIONOMICS: Males occur in swarms flying low along the banks about a foot off the water. [Larvae probably in shallow acidic seepage pools or hoof-prints.]

259. *Dixa distincta* Garrett, 1925a:12. TYPE: Holotype ♂ (130), St. Joseph Creek, Cranbrook, British Columbia, 16 Oct, C. Garrett (CNC).

260. *Dixa fluvica* Peters, 1966:242-243. TYPE: Holotype ♂, Valley Creek (Washington Co.), Minnesota, 3 July 1962, T.M. Peters (USNM, 67268). BIONOMICS: Adults swept from vegetation near stream. Larvae among duckweed and watercress in quiet backwater just below entrance of spring into clear, fast, rocky stream.

261. *Dixa fraterna* Garrett, 1924a:6. TYPE: Holotype ♂, Bull River, British Columbia, 10 Oct 1923, C. Garrett (CNC).

262. *Dixa fusca* Loew, 1863a:4. TYPE: Lectotype ♀, New York, probably collected by Osten Sacken (MCZ 10391, by PRESENT SELECTION; MCZ 10391 [2] here designated as paralectotype).

263. *Dixa mystica* Dyar & Shannon, 1924b:197-198 [=fusca]. TYPE: Lectotype ♂, Cabin John (Montgomery Co.), Maryland, 22 Feb 1915, R.C. Shannon (USNM, 27451, by PRESENT SELECTION; ♂ adult, Difficult Run (Fairfax Co.), Virginia, 3 Oct 1915, W.R. McAtee, USNM, 27451 is here designated paralectotype).

264. *Dixa hegemonica* Dyar & Shannon, 1924b:194-195. TYPE: Holotype ♂, Eureka (Humboldt Co.), California, 25 May 1903, H.S. Barber (USNM, 27446).

265. *Dixa inextricata* Dyar & Shannon, 1924b:198-199. TYPE: Lectotype ♂, (slide 2008), Dead Run (Fairfax Co.), Virginia, 25 Mar 1914, R.C. Shannon (USNM, 27452; selection of Peters and Cook, 1966:245).

266. *Dixa johannseni* Garrett, 1924a:7. TYPE: Holotype ♂, Michel, British Columbia, 21 Sept, C. Garrett (CNC). BIONOMICS: [Adults probably swarm above streams.]

267. *Dixa lobata* Garrett, 1924a:6. TYPE: Holotype ♂, Cranbrook, British Columbia, 30 June, C. Garrett (CNC).

268. *Dixa melanderi* Peters, 1966:246. TYPE: Holotype ♂, Puget, Washington, 4 July 1924, A. L. Melander (USNM, 67269).

269. *Dixa modesta* Johannsen, 1903b:429-431. TYPE: Lectotype ♂, Ithaca (Tompkins Co.), New York, Apr 1902, O.A. Johannsen (Cornell 2992, by PRESENT SELECTION). BIONOMICS: Larvae in slow flowing streams.

270. *Dixa neohegemonica* Peters, 1966:247. TYPE: Holotype ♂, Mill Valley (Marin Co.), California, 6 May 1936 (CAS).

271. *Dixa notata* Loew, 1863a:4. TYPE: Lectotype ♀, Maryland, probably collected by Osten Sacken (MCZ 10393, by PRESENT SELECTION; MCZ 10393 [2] is here designated paralectotype).

272. *Dixa pullogruma* Peters, 1966:248-249. TYPE: Holotype ♂, Rapid Creek, 2 mi E of Rochford (Pennington Co.), South Dakota, 14 Sept 1961, T.M. Peters et al. (USNM, 67270). BIONOMICS: Larvae in a fast, cold stream.

273. *Dixa repanda* Peters, 1966:249. TYPE: Holotype ♂, Goodhue Co., Minnesota, 21 May 1937, D.G. Denning (USNM, 67271).

274. *Dixa rhathyme* Dyar & Shannon, 1924b:197. TYPE: Holotype ♂, Glacier (Whatcom Co.), Washington, 4 June 1917, H. B. Dyar (USNM, 27450).

275. Dixa montana Garrett, 1924a:5; garretti Cooper & Rapp, 1944:247, new name [= rhathyme]. TYPE: Holotype ♂, Cranbrook, British Columbia, 30 June, C. Garrett (CNC).

276. Dixa parva Garrett, 1924a:6. [= rhathyme]. TYPE: Holotype ♂, Wasa, British Columbia, Oct, C. Garrett (CNC).

277. Dixa rudis Garrett, 1924a:6. TYPE: Holotype ♂, Ta Ta Creek, Wasa, British Columbia, 27 Sept, C. Garrett (CNC).

278. Dixa similis Johannsen, 1923a:57-58. TYPE: Holotype ♂, Ithaca (Tompkins Co.), New York, Aug, O.H. Johannsen (Cornell 2993).

279. Dixa terna Loew, 1863a:3. TYPE: Lectotype ♂, New York, probably collected by Osten Sacken (MCZ 10394, by PRESENT SELECTION; MCZ 10394 [2] is here designated as paralectotype).

280. Dixa venosa Loew, 1872a:50. TYPE: Holotype ♀, Belfrage, Texas (MCZ 10395).

281. Dixa xavia Dyar & Shannon, 1924b:195-196. TYPE: Holotype ♂, Los Gatos (Santa Clara Co.), California, 16 Feb 1906, J.M. Aldrich (USNM, 27448).

282. Dixella aliciae (Johannsen, 1924b:45-46). TYPE: Holotype ♂, Claremont, across street E from High School (Los Angeles Co.), California, 1 May 1923, Alica M. Westfall (Cornell 2995). BIONOMICS: Reared from larvae collected from surface of pool formed by leak in irrigation pipe.

283. Dixella aurora Peters, 1966:254-255. TYPE: Holotype ♂, swamp, Ringwood Reservoir (Tompkins Co.), New York, 16-17 June 1963, W.W. Wirth (USNM, 67272).

284. Dixella californica (Johannsen, 1923a:54-55). TYPE: Holotype ♂, Stanford University (Santa Clara Co.), California, Mar (Cornell 2770). BIONOMICS: [Larvae probably in clear, shallow, eurythermous, acidic pools with muddy bottoms and emergent vegetation.]

285. Dixella thones (Dyar & Shannon, 1924b:193-194) [= californica]. TYPE: Lectotype ♂, Longmire Springs [Mt. Rainier Nat. Park], Washington, 2 Aug 1905, J.M. Aldrich (USNM, 27445, slide 2028, by PRESENT SELECTION; USNM, 27445, 14 June 1917, H.G. Dyar, is here designated paralectotype).

286. Dixella clavata (Loew, 1869b:2). TYPE: Lectotype ♀, Lenox (Berkshire Co.), Massachusetts, Osten Sacken (MCZ 10390, by PRESENT SELECTION; MCZ 10390 [2] is here designated a paralectotype.)

287. Dixella cornuta (Johannsen, 1923a:55-56). TYPE: Holotype ♂, McLean (Tompkins Co.), New York, Oct (Cornell 2990). BIONOMICS: [Larvae probably in permanent open or temporary woodland ponds, acidic to neutral, less than 6 feet deep, 11-28°C, with muddy or leafy bottom. May also occur in slow to fast, shallow, slightly acidic, 14-22°C stream.]

288. Dixella plexipus (Garrett, 1925b:5) [= cornuta]. TYPE: Holotype ♂ (150), Nelson, British Columbia, June, C. Garrett (CNC).

289. Dixella simplex (Garrett, 1925a:12) [= cornuta]. TYPE: Lectotype ♂, Cranbrook, British Columbia, June, C. Garrett (CNC; by PRESENT SELECTION).

290. Dixella somnolenta (Dyar & Shannon, 1924b:195) [= cornuta]. TYPE: Holotype ♂, Viola (Latah Co.), Utah, 21 Aug 1912, J.M. Aldrich (USNM, 27447).

291. Dixella spiralis (Garrett, 1924a:1-2) [= cornuta]. TYPE: Lectotype ♂, Wasa, British Columbia, 22 Oct 1923, C. Garrett (CNC 5332, by PRESENT SELECTION; ♂, Wasa, British Columbia, 25 Oct 1923 (CNC 5341); ♂, Wasa, British Columbia, 21 Oct 1923; ♂, Wasa, British Columbia, 23 Oct 1923;

♂, Cranbrook, British Columbia, 2 July 1920 (CNC 2618); ♂, Cranbrook, British Columbia, 21 Oct 1923 (CNC 5511) are here designated paralectotypes).

292. *Dixella deltoura* Peters, 1966:257-258. TYPE: Holotype ♂, Nenana, Alaska, 13 June 1951, R.I. Sailor (USNM, 67274).

293. *Dixella dorsalis* (Garrett, 1924a:4). TYPE: Holotype ♂, Wasa, British Columbia, 23 Oct, C. Garrett (CNC). BIONOMICS: [Larvae probably in shallow bogs, seepage pools, temporary woodland pools, or permanent open ponds with a temperature range of 13-23°C, muddy or leafy bottoms, and 5.0-6.2 pH. Larvae probably situated at bases of sphagnum or sedge hummocks. Larvae may also occur in large, slow streams less than 4 ft. deep, with a pH range of 6.2-7.0, clear, and with a muddy or sandy rock bottom.]

294. *Dixella dyari* (Garrett, 1924a:3). TYPE: Holotype ♂, Cranbrook, British Columbia, 25 June, C. Garrett (CNC).

295. *Dixella indiana* (Dyar, 1925:217-218). TYPE: Holotype ♂, Fort Benjamin Harrison (Marion Co.), Indiana, 23 June 1925, H.K.B. Hufford (USNM, 28419). BIONOMICS: [Larvae probably in clear to slightly turbid seepage pools in slow to moderately fast, clear to rust-colored streams with a range of temperature of 15.5-23.5°C, pH 5.5-8.0, depth of 10 inches-5 feet, muddy to rocky bottom. Adults probably swarm at edges of stream at twilight.]

*296. *Dixella marginata* (Loew, 1863a:2). TYPE: Holotype ♀, District of Columbia, Osten Sacken (MCZ 10392).

297. *Dixella neoaliciae* (Garrett, 1924a:2-3). TYPE: Holotype ♂, Bozeman (Gallatin Co.), Montana, 3 Sept, C. Garrett (CNC). BIONOMICS: [Larvae probably in eddies of cold, clear, slightly acidic streams or in warm, clear, slightly acidic ponds less than 3 feet deep and with silted bottom. Adults probably rest in emergent vegetation during the day.]

298. *Dixella nova* (Walker, 1848:85). TYPE: ♂, New York Factory, [Hudson's Bay at mouth of Hayes River, Manitoba] (BM). BIONOMICS: [Larvae probably in shallow, rust-colored bogs and clear temporary woodland pools or seepage pools with leafy bottoms, a temperature range of 13-17.5°C and pH of 6.0-6.8.]

299. *Dixella centralis* (Loew, 1863a:3) [=nova]. TYPE: Holotype ♂, New York, Osten Sacken (MCZ 10389). Terminalia of the type is missing.

300. *Dixella nocheles* (Dyar & Shannon, 1924b:196-197) [=nova]. TYPE: Holotype ♂, Biscayne Bay (Dade Co.), Florida, probably A.T. Slossen (USNM, 27449).

301. *Dixella occidentalis* (Garrett, 1924a:4-5) [=nova]. TYPE: Holotype ♂, Gold Creek, Cranbrook, British Columbia, 1 May, C. Garrett (CNC).

302. *Dixella serrata* (Garrett, 1924a:2). TYPE: Holotype ♂, Oliver, British Columbia, 6 May, C. Garrett (CNC). BIONOMICS: [Larvae probably in shallow ponds or very slow-moving streams with silt bottoms, a temperature range of 14.5-28°C and pH of 6.8-7.0. Infrequently larvae may be found in clear, fast, warm, rocky, very acidic streams.]

303. *Dixella techana* Peters, 1966:263. TYPE: Holotype ♂, Hassayampa River, Wickenburg (Maricopa Co.), Arizona, 29 June 1953, W.W. Wirth (USNM, 67275). BIONOMICS: [Larvae probably in clear, warm, alkaline, shallow stream with current less than 50 ft/min. and a rocky bottom.]

304. *Dixella universitatis* (Cockerell, 1926:166). TYPE: Holotype ♀, Boulder (Boulder Co.), Colorado, 27 Sept 1926, Scott Gale (USNM, 29540).

305. *Dixella vespertina* Peters, 1966:264. TYPE: Holotype ♂, McFadden Pond, Corvallis (Benton Co.), Oregon, 17 Sept 1953, V. Roth (Oregon State Univ.).

*306. Meringodixa chalonensis Nowell, 1951:299. TYPE: Lectotype ♂, Chalone Creek [Pinnacles Nat. Monument], California, 20 Apr 1950, W.R. Nowell (USNM, by PRESENT SELECTION). BIONOMICS: Larvae in protected, shaded spots among rocks in stream.

Nomen Dubium

307. Dixa recens Walker, 1848:85. TYPE: ♀, New York Factory [Hudson's Bay at mouth of Hayes River, Manitoba]; type lost and the description is inadequate for determination of the taxonomic species involved (Peters and Cook, 1966:251).

LIST OF LOCALITIES

Canada

BRITISH COLUMBIA

Bull River: 261. Dixa fraterna.

Cranbrook: 259. Dixa distincta; 267. Dixa lobata; 294. Dixella dyari; 275. Dixella garretti; 301. Dixella occidentalis; 289. Dixella simplex; 291. Dixella spiralis.

Michel: 266. Dixa johannseni.

Nelson: 288. Dixella plexipus.

Okanagan Falls: 258. Dixa brevis.

Oliver: 302. Dixella serrata.

Wasa: 276. Dixa parva; 277. Dixa rudis (Ta Ta Creek); 293. Dixella dorsalis.

MANITOBA

New York Factory (Hudson's Bay at mouth of Hayes River): 298. Dixella nova; 307. Dixa recens.

United States

ALASKA

Nenana: 292. Dixella deltoura.

ARIZONA

Bright Angel (Coconino Co.): 257. Dixa blax.

Wickenburg, Hassayampa River (Maricopa Co.): 303. Dixella techana.

CALIFORNIA

Chalone Creek (San Benito Co.): 306. Meringodixa chalonensis.

Claremont (Los Angeles Co.): 282. Dixella aliciae.

Eureka (Humboldt Co.): 264. Dixa hegemonica.

Los Gatos (Santa Clara Co.): 281. Dixa xavia.

Mill Valley (Marin Co.): 270. Dixa neohegemonica.

Stanford University (Santa Clara Co.): 284. Dixella californica.

COLORADO

Boulder (Boulder Co.): 304. Dixella universitatis.

DISTRICT OF COLUMBIA

Washington: 296. Dixella marginata.

FLORIDA

Biscayne Bay (Dade Co.): 300. Dixella nocheles.

IDAHO

Viola (Latah Co.): 290. Dixella somnolenta.

INDIANA

Fort Benjamin Harrison (Marion Co.): 295. Dixella indiana.

MARYLAND

Cabin John (Montgomery Co.): 263. Dixa mystica.

Locality not specified: 271. Dixa notata.

MASSACHUSETTS

Lenox (Berkshire Co.): 286. Dixella clavata.

MINNESOTA

Valley Creek (Washington Co.): 260. Dixa fluvica.

Goodhue Co.: 273. Dixa repanda.

MONTANA

Bozeman (Gallatin Co.): 297. Dixella neoaliciae.

NEW YORK

Ithaca (Tompkins Co.): 269. Dixa modesta; 278. Dixa similis.

McLean (Tompkins Co.): 287. Dixella cornuta.

Ringwood Reservoir (Tompkins Co.): 283. Dixella aurora.

Locality not specified: 262. Dixa fusca; 279. Dixa terna; 299. Dixella centralis.

OREGON

Corvallis, McFadden Pond (Benton Co.): 305. Dixella vespertina.

SOUTH DAKOTA

Rapid Creek (Pennington Co.): 272. Dixa pullogruma.

TEXAS

Belfrage: 280. Dixa venosa.

VIRGINIA

Dead Run (Fairfax Co.): 265. Dixa inextricata.

WASHINGTON

Glacier (Whatcom Co.): 274. Dixa rhathyme.

Mt. Rainier National Park, Longmire Springs: 256. Dixa arge; 285. Dixella thones.

Puget: 268. Dixa melanderi.

REFERENCES CITED

The citations of author, date and page in the List of Species refer to the bibliography in "A Catalog of the Diptera of America North of Mexico" (U. S. D. A. Agricultural Handbook No. 276, 1965).

Belkin, J. N., R. X. Schick and S. J. Heinemann

1966. Mosquito Studies (Diptera, Culicidae). VI. Mosquitoes originally described from North America. Amer. Entomol. Inst., Contrib. 1(6). 39 p.

Peters, T. M.

1966. [Descriptions of new species] In Peters, T. M. and E. F. Cook, 1966 (see below).

Peters, T. M. and E. F. Cook

1966. The Nearctic Dixidae (Diptera). Entomol. Soc. Amer., Misc. Publications 5(5):231-278. 23 Dec.

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MOSQUITO STUDIES (Diptera, Culicidae)

XI. MOSQUITOES ORIGINALLY DESCRIBED FROM ARGENTINA, BOLIVIA, CHILE, PARAGUAY, PERU, AND URUGUAY¹

By

John N. Belkin, Robert X. Schick and Sandra J. Heinemann²

This is the fourth in a series of papers providing information on the source of the original type material of mosquitoes described from the Americas (Belkin, Schick and Heinemann, 1965, 1966; Peters, 1968). The concluding paper on species described from Brazil and unspecified localities in South America is in preparation. For explanation of the arrangement and method of presentation, the first paper of the series should be consulted.

We are most grateful to Osvaldo H. Casal of the Instituto Nacional de Microbiología, Buenos Aires, for his careful study of the type material in Argentina and for allowing us to publish his lectotype designations in this paper. We also thank Alan Stone for information on material contained in the U.S. National Museum.

ARGENTINA

List of Species

1. Anopheles (A.) annulipalpis Lynch Arribálzaga, 1878. TYPE: ♀, Baradero (Buenos Aires), Apr 1878 (NE, according to O.H. Casal). BIONOMICS: [Larvae in semipermanent turbid ground water with scanty vegetation.]

2. Anopheles (A.) holmbergi Del Ponte & Heredia, 1945 [=fluminensis]. TYPE: Holotype ♂ (378) with genitalia slide (2293), Corpus, San Ignacio (Misiones), May 1944, R. L. Heredia (INM). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

*3. Anopheles (A.) argentinus (Brèthes, 1912) [=pseudopunctipennis]. TYPE: Lectotype ♂, bearing label by Brèthes, //Proterorhynchus argentinus Brèthes, type, Tucumán// (BA; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: [Larvae in small streams in mountains and foothills; water fresh, with moderate flow, and containing algae.]

¹Contribution from project "Mosquitoes of Middle America" supported by Public Health Service Research Grant AI-04379 and U.S. Army Medical Research and Development Command Research Contract DA-49-193-MD-2478.

²Department of Zoology, University of California, Los Angeles, California 90024.

4. Anopheles (A.) tucumanus Lahille, 1912 [=pseudopunctipennis]. TYPE: Holotype ♀, Río Salí (Tucumán), Dinelli (NE, according to O.H. Casal). BIONOMICS: [As for 3. argentinus.]

5. Anopheles (A.) patersoni Alvarado & Heredia, 1947 [=ssp. of pseudopunctipennis]. TYPE: Eggs, Tucumán (probably NE, according to O.H. Casal). BIONOMICS: [As for 3. argentinus.]

*6. Anopheles (Nyssorhynchus) albitarsis Lynch Arribálzaga, 1878. TYPE: ♀, Baradero (Buenos Aires) [NE; original type material lost; redescription by Umana, Heredia and Siquot (1960:609-618) from type locality does not constitute a neotype designation, this material also lost]. BIONOMICS: [Larvae usually in mats of aquatic vegetation in large ponds, marshes and lagoons of overflowing rivers, and in large sunlit ground pools with vegetation.]

7. Anopheles (N.) rooti (Brèthes, 1926) [=argyritarsis]. TYPE: ♂, Tucumán, N.C. Davis; only remaining material genitalia slide in poor condition, without sidepiece, with Brèthes label, "Cellia Rooti Brèthes=argyritarsis auct. (nec R.D.), Tucumán, N.C. Davis dedit, III.1956" (BA). BIONOMICS: [Larvae in all types of sunlit and partially shaded ground waters.]

8. Anopheles (N.) evansae (Brèthes, 1926). TYPE: Lectotype ♂ genitalia slide found in INM (returned to BA), with following Brèthes label, "Cellia evansi Brèthes=tarsimaculata auct. (nec Goeld), Tucumán, N.C. Davis ded., III. 1926, Pr. micr. An.M., " in Del Ponte's hand "384" "DP14," "DP14=?noroestensis G. y L., 1938, [signature in ink], Tipo de evansi [signature in black pencil] (BA; PRESENT DESIGNATION of O.H. Casal). BIONOMICS: [Larvae in marshes and marshy margins of clear freshwater pools, streams and lakes.]

9. Anopheles (N.) clarki Komp, 1943 [=noroestensis]. TYPE: Holotype ♂ with genitalia slide, Monteros (Tucumán), June 1940, C.A. Alvarado (USNM, 56476; apparently lost, not mentioned in Stone and Knight, 1956b). BIONOMICS: [Larvae probably in shaded fresh water in wooded swamps, pools or stagnant streams.]

*10. Anopheles (N.) bachmanni Petrocchi, 1925 [=ssp. of triannulatus]. TYPE: ♂, ♀, Corrientes, Entre Rios, Formosa (NE, according to O.H. Casal). BIONOMICS: [Larvae probably in freshwater pools and lakes, and along river margins, associated with vegetation.]

11. Anopheles (N.) perezi Shannon & Del Ponte, 1928 [=triannulatus bachmanni]. TYPE: ♀, [Finca] Santa Bárbara, Departamento de la Capital (Tucumán) (NE, according to O.H. Casal). BIONOMICS: Larvae in a lake.

12. Anopheles (N.) davisii Paterson & Shannon, 1927 [=triannulatus bachmanni]. TYPE: ♂, ♀, larvae, Tres Pozos, [near] Embarcación (Salta), 19-21 Apr 1927, Paterson, Shannon and Shannon (USNM, see Stone and Knight, 1956b: 277; INM, 1 ♀ with Shannon's labels, "House, Embarcación, Salta, 21.4.27, R.C. Shannon/Anopheles (Nyssorhynchus) davisii Pat. & Snn (Cotype)"). BIONOMICS: Larvae in very large masses of green algae in a lake.

13. Toxorhynchites (Lynchiella) cavalierii García & Casal. TYPE: Holotype ♀ with associated larval and pupal skins (c94), Puerto Iguazú about 50 m from the Hostería Ruffino (Igu 15) (Misiones), 25 June 1965, Casal, Hepper and García (INM). BIONOMICS: Larvae in a bromeliad 1 m above the ground.

14. Toxorhynchites (L.) tucumanus (Brèthes, 1926) [=guadeloupensis]. TYPE: Lectotype ♂ (1 of 6 with type labels) with following Brèthes labels, "Tucumán, 10-VII-926, E.G. Cabarro/elevé chez moi/Megarhinus tucumanus Brèthes" (BA; PRESENT DESIGNATION of O.H. Casal). BIONOMICS: [Larvae in leaf axils of bromeliads.]

15. Toxorhynchites (L.) arborealis (Shannon & Del Ponte, 1928) [=guade-

loupensis]. TYPE: ♀, Lules (Tucumán), Shannon and Del Ponte, 22 Mar 1927 [NE, according to O.H. Casal]. BIONOMICS: Larvae in a treehole.

16. Toxorhynchites (L.) separatus (Lynch Arribáizaga, 1891) [=ssp. of haemorrhoidalis]. TYPE: Lectotype ♂ with Lynch label "Megarrhina separata n.sp." and Del Ponte label "Megarrhinus haemorrhoidalis Fabr., D. P., X-49," according to original description collected in Formosa by E. L. Holmberg (BA; PRESENT DESIGNATION by O.H. Casal). BIONOMICS: [Larvae probably in leaf axils of bromeliads.]

17. Toxorhynchites (L.) lynchi (Dyar & Knab, 1906) [= haemorrhoidalis separatus]. TYPE: Lectotype ♂, only specimen in collection with Lynch's label, "Megarrhina haemorrhoidalis Fabr.," also with Del Ponte's label, "Megarrhinus lynchi tipo, D. P. X-49," according to original description collected in Formosa by E. L. Holmberg (BA; PRESENT DESIGNATION by O.H. Casal). BIONOMICS: [As for 16. haemorrhoidalis separatus.]

18. Trichoprosopon (Runchomyia) paranensis (Brèthes, 1910) [Distinct species, according to O.H. Casal]. TYPE: Lectotype ♀, the better of the 2 specimens bearing the following label, "Tuyuparé, 25.I.1908, J. B./Lynchiaria paranensis" (BA; PRESENT DESIGNATION by O.H. Casal). BIONOMICS: [Larvae probably in leaf axils of cattails, Typha.]

19. Wyeomyia (Nunezia) lateralis Petrocchi, 1927. TYPE: ♀, Zapla (Jujuy), 16 Mar 1916, A. Neiva (NE, according to O.H. Casal). BIONOMICS: [Larvae probably in leaf axils of bromeliads.]

*20. Wyeomyia (Davismyia) petrocchiae (Shannon & Del Ponte, 1928). TYPE: Holotype ♀, Raco (Tucumán), 13 Feb 1927, Shannon and Del Ponte (USNM; see Stone and Knight, 1957b:126). BIONOMICS: [Larvae probably in treeholes.]

21. Wyeomyia (Davismyia) monoleua (Martini, 1931) [= petrocchiae]. TYPE: Holotype ♀, San José (Formosa), Oct 1925 (SMNS). BIONOMICS: [Larvae probably in treeholes.]

22. Wyeomyia (Menolepis) leontinae (Brèthes, 1910) [= leucostigma]. TYPE: Lectotype ♀, the best of the 5 ♀, all without type label and all bearing Brèthes labels, "Tuyuparé, 25-I-1908, J. B" and "Limatus Leontinae" (BA; PRESENT DESIGNATION of O.H. Casal). BIONOMICS: [Larvae probably in leaf axils of cattails, Typha.]

23. Wyeomyia (Dendromyia) belkini Casal & García, 1966. TYPE: Holotype ♂ with genitalia, larval and pupal skins (C57), intersection of the arroyo Ibicuy and route 101, about 20 km west of Cataratas (Igu 26) (Misiones), 26 June 1965, Hepper, García and Casal (INM). BIONOMICS: Adults taken in the forest interior during the day, probably attracted to a human host. Larvae in bamboo internodes.

24. Wyeomyia (D.) typharum (Shannon & Del Ponte, 1928) [= melanocephala]. TYPE: Lectotype ♀, bearing label probably in Del Ponte's hand "Dendromyia typharum" and also with following labels (present on other ♀), "Jujuy, Ledesma, 3.19.26/Davis and Shannon/49036" and "Metatypus" (BA; PRESENT DESIGNATION of O.H. Casal). BIONOMICS: Larvae in leaf axils of cattails, Typha.

25. Phoniomyia muehlensi (Petrocchi, 1927). TYPE: Holotype, sex unknown, Chaco, Oct-Nov 1924, J. Petrocchi (NE, according to O.H. Casal). BIONOMICS: [Larvae in leaf axils of bromeliads.]

26. Limatus exhibitor Shannon & Del Ponte, 1928 [= durhamii]. TYPE: Lectotype ♂ with following label, "Iguazú, Mis.[iones] 18.6.27, Shannon & Del Ponte" and in Shannon's hand, "Limatus exhibitor Snn & D. P" (INM; PRESENT DESIGNATION of O.H. Casal). BIONOMICS: [Larvae in broken bamboo and in artificial containers at the type locality (O. H. Casal).]

27. Sabethes (S.) neivai Petrocchi, 1927 [= albiprivus]. TYPE: Holotype ♀, Santa Clara (Jujuy), May 1916, Arturo Neiva (NE, according to O.H. Casal). BIONOMICS: [Larvae probably in treeholes or bamboo internodes.]

28. Coquillettidia (Rhynchotaenia) fasciolata (Lynch Arribáizaga, 1891). TYPE: Originally described from ♀ from Navarro (Buenos Aires), Mar 1886, F. Lynch (NE), neotype ♀, Parque Lezama, Capital Federal (Buenos Aires), 13 Dec 1928, Carillo (INM; designation of Castro and Bressanello, 1952:232). BIONOMICS: [Larvae probably on rootlets of grasses and herbaceous vegetation in mud and fine sediment in very shallow water on the margins of swamps, ponds or streams.]

29. Coquillettidia (Rhynchotaenia) araozi (Shannon & Del Ponte, 1928) [= venezuelensis]. TYPE: ♀, Ledesma (Jujuy), 20 Mar 1926, Davis and Shannon; no specimens of type series in BA, according to O.H. Casal (USNM; lectotype to be designated by Alan Stone). BIONOMICS: [Larvae probably as for 28. fasciolata.] ♀ taken on animal bait.

30. Uranotaenia lanei Martínez & Prosen, 1953. TYPE: Holotype ♀, Formosa (BA, according to O.H. Casal). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

31. Uranotaenia monilis Shannon & Del Ponte, 1928. TYPE: Lectotype ♀ bearing the labels "Resistencia, Chaco, 20.2.27, R.C. Shannon/Uranotaenia monilis Snn. & D.P." in Shannon's hand (INM; PRESENT DESIGNATION by O.H. Casal). BIONOMICS: [Larvae probably in large lowland swamps or in other sunlit ground waters with some aquatic vegetation.]

*32. Uranotaenia nataliae Lynch Arribáizaga, 1891. TYPE: Lectotype adult, only the thorax and first abdominal segment remaining, with a label by Lynch "Uranotaenia nataliae n.sp., Tigre" [at the confluence of the Río Las Conchas and Río Paraná (Buenos Aires), Enrique Lynch, brother of Félix] (BA; PRESENT DESIGNATION by O.H. Casal). BIONOMICS: [Larvae probably in large open swamps with abundant aquatic vegetation such as Pistia and sedges.]

33. Uranotaenia capitis Shannon & Del Ponte, 1928. TYPE: Holotype ♀, Ledesma (Jujuy), 20 Mar 1926, Davis (USNM). BIONOMICS: [As for 32. nataliae.]

*34. Uranotaenia pulcherrima Lynch Arribáizaga, 1891. TYPE: ♂, [probably] bank of Río Luján (Buenos Aires), E. L. Holmberg (NE, according to O.H. Casal). BIONOMICS: [Larvae probably in swamps, stream margins or other permanent ground waters.]

35. Uranotaenia urania Shannon & Del Ponte, 1928 [= pulcherrima]. TYPE: Lectotype ♂ (2355) with genitalia slide, Resistencia (Chaco), 20 Feb 1927, Shannon and Del Ponte (USNM, designation of Stone and Knight, 1957c:200). BIONOMICS: [As for 34. pulcherrima.]

36. Uranotaenia elnora Paterson & Shannon, 1927 [ssp. of pulcherrima]. TYPE: Holotype ♀, Tres Pozos near Embarcación (Salta), 19 Apr 1927, Elnora S. Shannon (USNM). BIONOMICS: [Probably as for 34. pulcherrima.]

*37. Aedeomyia squamipennis (Lynch Arribáizaga, 1878). TYPE: ♂, ♀, Baradero (Buenos Aires), Apr 1878, F. Lynch (NE, according to O.H. Casal). BIONOMICS: [Larvae in lakes, ponds and permanent ground pools with abundant vegetation and algae.]

38. Psorophora (P.) lynchi Brèthes, 1916 [= ciliata]. TYPE: Lectotype ♀, the best of the 4 female syntypes in the BA, and in good condition, bearing the labels "B.[uenos] Aires, 20.II.1916, J.B./Psorophora Lynchi Br." (the other 3 females are similarly labeled) (BA; PRESENT DESIGNATION by O.H. Casal). BIONOMICS: [Larvae probably in unshaded temporary rain pools.]

39. Psorophora (P.) holmbergii Lynch Arribálzaga, 1891. TYPE: Lectotype ♀, the one specimen in the collection of the BA bearing the following label by F. Lynch, "Psorophora Holmbergi n.sp., Chaco" [Formosa], E. L. Holmberg (BA; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: [Larvae in temporary rain pools.]

40. Psorophora (P.) agoggylia Dyar, 1922 [=holmbergii]. TYPE: Lectotype ♀, Río Tapenaga, Colonia Florencia, Gran Chaco (Formosa [Santa Fe]), 1903, E. R. Wagner (USNM, 25756; designation of Stone and Knight, 1955:286). BIONOMICS: [Larvae probably in temporary rain pools.]

41. Psorophora (P.) stigmatophora Dyar, 1922 [=pallescens]. TYPE: Lectotype ♂ (1660) with genitalia slide, Río Tapenga, Colonia Florencia, Gran Chaco (Formosa [Santa Fe]), 1903, E. R. Wagner (USNM, 25756; designation by Stone and Knight, 1955:286). BIONOMICS: [Larvae probably in temporary rain pools.]

42. Psorophora (Janthinosoma) centrale Brèthes, 1910 [=ferox]. TYPE: Lectotype ♀ with the following labels, "Buenos Aires, 4. XII. 1907, B./Janthinosoma centralis [sic] Brèthes" in Brèthes' hand, type locality cited as "Islas del Paraná, Buenos Aires" in the original description (BA; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: [Larvae probably in temporary rain and floodwater pools in wooded areas.]

43. Psorophora (J.) chaquensis Paterson & Shannon, 1927 [=lutzii]. TYPE: Holotype ♀, Tres Pozos, near Embarcación (Salta), 20 Apr 1927, probably Paterson and Shannon (NE, according to Casal). BIONOMICS: [Larvae probably in temporary rain and floodwater pools in wooded areas.]

44. Psorophora (J.) bruchi Petrocchi, 1927 [=varipes]. TYPE: ♂, ♀, Provincia de Buenos Aires, 1 Apr 1925, C. Bruch (NE, according to O. H. Casal). BIONOMICS: [Larvae probably in temporary rain and floodwater pools in wooded areas.]

*45. Psorophora (Grabhamia) confinnis Lynch Arribálzaga, 1891. TYPE: Lectotype ♀, the only female of the original 5 specimens remaining in the BA, in fairly good condition, with the following label by F. Lynch, "Taeniorhynchus confinnis F. Lch., Chaco [Formosa]," E. L. Holmberg (BA; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: [Larvae probably in open temporary ground pools of all types, especially hoofprints and road ruts.]

46. Psorophora (G.) paulli (Paterson & Shannon, 1927). TYPE: Lectotype ♀, proboscis broken, 2 legs missing and abdomen glued on a card, with the following labels in Shannon's handwriting, "Tres Pozos, Salta, 20.4.27, Shannon & Snn/Types Psorophora Paulli Paterson & Shannon" (INM; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: [Larvae probably in temporary ground pools or overflows of ponds or streams.]

47. Aedes (O.) meprai Martínez & Prosen, 1953 [=angustivittatus]. TYPE: Holotype ♀, Reserva Nacional "Finca del Rey," Departamento de Anta (Salta), Nov 1952, Martínez and Prosen (BA). BIONOMICS: [Larvae in temporary rain pools.] Adults captured on human bait in daytime in forest.

48. Aedes (Ochlerotatus) lynchii (Brèthes, 1910) [=crinifer]. TYPE: Lectotype ♀, the best of 9 females, in fairly good condition, all from Buenos Aires with the following labels, "6139/Buenos Aires, J. Brèthes 19.I.1903/Culex Lynchii Br.," the latter two by Brèthes (BA; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: [Larvae probably in temporary rain pools.]

49. Aedes (O.) tapinops (Brèthes, 1917) [=crinifer]. TYPE: Lectotype ♂, in fairly good condition, with the following labels by Brèthes, "S. Isidro [Buenos Aires], II.2.1917. J. B./Culex tapinops Bret." (BA; PRESENT DESIGNATION

by O. H. Casal). BIONOMICS: [Larvae probably in temporary rain pools.]

50. Aedes (O.) iguazu Shannon & Del Ponte, 1928 [=crinifer]. TYPE: ♂, ♀ [Cataratas del Iguazú], Misiones (3 ♀, without type labels but collected at Iguazu Falls by Shannon and Shannon in Oct 1927, are present in the USNM; no specimens of the type series are in the INM). BIONOMICS: [Larvae probably in temporary rain pools.]

51. Aedes (O.) araozi Shannon & Del Ponte, 1928 [=milleri]. TYPE: Lectotype ♂, in fairly good condition, with the following labels in Shannon's hand, "Quebrada San Lorenzo, Salta, 4.VIII.27, R. C. Shannon/A. 154/Aedes araozi Shannon & Del Ponte," with genitalia slide (655) (INM; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: Larvae in a small rockhole covered with dead leaves very near a small torrential stream.

52. Aedes (O.) patersoni Shannon & Del Ponte, 1928. TYPE: Lectotype ♀, in very bad condition, a mesothoracic leg and an antenna are missing and the mesonotum is largely rubbed, with the following labels, "San Pedro de Jujuy, 27.4.26/Inst. Bac. Ent. nota 44/Shannon and Shannon" (INM; PRESENT DESIGNATION by O. H. Casal; the same specimen improperly designated as Holotype by García & Ronderos, 1963:32). BIONOMICS: Larvae in a temporary swampy area formed by rains.

53. Aedes (O.) raymondi Del Ponte, Castro & García, 1951. TYPE: Holotype ♀ (587), San Pedro (Jujuy), 27 Apr 1926, Shannon and Shannon (INM). BIONOMICS: [Larvae probably in temporary rain pools.]

*54. Aedes (O.) confirmatus (Lynch Arribáizaga, 1891) [=scapularis]. TYPE: Lectotype ♀, in good condition, with the following labels by F. Lynch, "Ochle-rotatus cofirmatus [sic], F Lynch, Navarro [Buenos Aires]," May 1887 (BA; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: [Larvae in temporary rain pools.]

55. Haemagogus (Stegoconops) petrocchiaie Martínez, Carcavallo & Prosen, 1961 (=ssp. of capricornii). TYPE: Holotype ♂, Salvador Mazza (Pocitos), Departamento General San Martín (Salta), Jan 1960, Martínez and Carcavallo (BA). BIONOMICS: Females taken biting on human bait at dusk and at night in woods without artificial lights. [Larvae probably in treeholes.]

56. Haemagogus (Stegoconops) spegazzinii Brèthes, 1912. TYPE: Holotype ♀ [with the following labels, "No 7273/Jujuy/Haemagogus spegazzinii Brèthes" and 2 slides (3028), one with a wing and the other with genitalia, an antenna and a palpus], Jujuy, 1907, D. Carlos Spegazzini (BA). BIONOMICS: [Larvae probably in treeholes.] Adult(s) taken in deep woods.

57. Haemagogus (Stegoconops) uriartei Shannon & Del Ponte [=spegazzinii]. TYPE: Holotype ♂ (128-3) with genitalia slide (2353) and pupal skin slide (V 3), Vipos (Tucumán), 22 Mar 1927, Shannon and Del Ponte (USNM; see Stone and Knight, 1955:289). BIONOMICS: Holotype bred from larva in a treehole.

58. Culex (Lutzia) patersoni Shannon & Del Ponte, 1928 [=bigoti]. TYPE: Lectotype ♂ (2356) with genitalia slide, San Pedro (Jujuy), 27 Apr 1926, Shannon and Shannon (USNM; designation of Stone and Knight, 1957a:54). BIONOMICS: [Larvae in ground pools, rockholes and artificial containers.]

59. Culex (C.) ameliae Casal, 1967. TYPE: Holotype ♂, with associated larval and pupal skins (Ga 137-31), San Pedro-El Dorado road, about 10 km from San Pedro (Misiones), 11 Mar 1966, García and Casal (INM). BIONOMICS: Larvae in an extensive flooded depression in the middle of the forest crossed by the road.

60. Culex (C.) interfor Dyar, 1928 [=bidens]. TYPE: Lectotype ♂ (532) with genitalia slide (2364), in train between Tucumán and Jujuy (Jujuy, Salta or

Tucumán), 4 May 1927, M. Kisliuk Jr. (USNM; designation by Stone and Knight 1957a:51). BIONOMICS: [Larvae probably in permanent and semipermanent ground waters.] Adults taken at light on train.

61. Culex (C.) brethesi Dyar, 1919. TYPE: Holotype ♂ (on slide with the genitalia and a female) [San Isidro (Buenos Aires), Apr or May 1916] (BA). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

62. Culex (C.) castroi Casal & García, 1967. TYPE: Holotype ♂ with associated larval and pupal skins (Ga 289-11), Canal 6 and Paraná de las Palmas, Estación Agropecuaria Delta del I. N. T. A. (near Otamendi) (Buenos Aires), 27 July 1966, García and Casal (INM). BIONOMICS: Larvae in leaf axils of Eryngium sp.

*63. Culex (C.) dolosus (Lynch Arribáizaga, 1891). TYPE: Lectotype ♂, in very bad condition, partially covered by fungi, the head and the posterior abdominal segments missing, with the following label by F. Lynch, "Heteronychia dolosa n. sp.," no locality label, the following 5 localities given in the original description: Las Conchas, Zárate, Baradero, Navarro and Chacabuco (all Buenos Aires) (BA; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: [Larvae in permanent and semipermanent ground waters.]

64. Culex (C.) bonariensis Brèthes, 1916 [= dolosus]. TYPE: Lectotype ♂, with type label but without locality label, and genitalia slide (V) [San Isidro (Buenos Aires)], May (BA; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: [Probably as for 63. dolosus.]

65. Culex (C.) eduardoi Casal & García, 1968. TYPE: Holotype ♂ with associated larval and pupal skins (Ga 314-17), Canal 6 and Paraná de las Palmas, Estación Agropecuaria Delta de I. N. T. A. (near Otamendi) (Buenos Aires), 10 Aug 1966, García and Casal (INM). BIONOMICS: Larvae in a marshy depression.

66. Culex (C.) fernandezi Casal, García and Cavalieri, 1966. TYPE: Holotype ♂ with associated larval and pupal skins (Ga 85-15), stream in Piquirenda (Salta), 26 Nov 1965, Fernandez, Hepper, García and Casal (INM). BIONOMICS: Larvae in axils of epiphytic or terrestrial bromeliads.

67. Culex (C.) hepperi Casal & García, 1967. TYPE: Holotype ♂ with associated larval and pupal skins (Ga 268-10), Canal 6 and Paraná de las Palmas, Estación Agropecuaria Delta de I. N. T. A. (near Otamendi) (Buenos Aires), 30 Apr 1966, García and Casal (INM). BIONOMICS: Larvae in leaf axils of Eryngium.

68. Culex (C.) lahillei Bachmann & Casal, 1962. TYPE: Holotype ♂ (1124) with genitalia slide (5219), Achiras (Córdoba), Mar 1938, Del Ponte (INM). BIONOMICS: [Larvae probably in permanent and semipermanent ground waters.]

69. Culex (C.) maxi Dyar, 1928. TYPE: Lectotype ♂ on slide 2360 and some legs on pin mount, San Pedro (Jujuy), 11 June 1927, M. Kisliuk Jr. (USNM; designation by Stone and Knight, 1957a:53). BIONOMICS: [Larvae in permanent and semipermanent ground waters.]

70. Culex (C.) autumnalis Weyenbergh, 1882 [= pipiens quinquefasciatus]. TYPE: ♂, ♀, larva, pupa, Río Primero (Córdoba) (? Universidad de Córdoba). BIONOMICS: [Larvae in large artificial containers and contaminated ground water.]

71. Culex (C.) saltanensis Dyar, 1928. TYPE: Holotype ♂, Campo Santo de Salta (Salta), 12 May 1927, M. Kisliuk Jr. (USNM). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

*72. Culex (Allimanta) tramazayguesi Duret, 1954. TYPE: Holotype ♂ (M.R. 110, E. 1), Monte Comán (Mendoza), 16 Dec 1953, Bejarano and Duret (CMPHM).

BIONOMICS: [Larvae found in hypersaline ground water near a thermal spring (Casal).]

73. Culex (Melanoconion) aliciae Duret, 1953. TYPE: Holotype ♂ (Mis. 13, E 8) with genitalia slide, Cerro Azul, Arroyo San Juan (Misiones), 2 May 1949, Bejarano and Duret (CMPHM). BIONOMICS: [Larvae probably in stream pools or other permanent or semipermanent ground waters.]

74. Culex (Mel.) bejaranoi Duret, 1953. TYPE: Holotype ♂ (A. U. 93, E. 20) with genitalia slide, Bernardo de Irigoyen (Misiones), 18 Mar 1951, Duret (CMPHM). BIONOMICS: [Larvae found in large ground pool in a probably flooded forest (Casal).]

75. Culex (Mel.) intricatus Brèthes, 1916. TYPE: Holotype ♂, lowlands of San Isidro (Buenos Aires), 15 May 1916, Brèthes (BA). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

76. Culex (Mel.) martinezi Casal & García, 1968. TYPE: Holotype ♂ with associated larval and pupal skins (Ga 418-17), km 34 of the Vespucio-San Pedrito road, near Vespucio (Salta), 6 Oct 1966, García, Hepper and Fernández (INM). BIONOMICS: Larvae taken at the margins of an arroyo.

77. Culex (Mel.) misionensis Duret, 1953. TYPE: Holotype ♂ (A.U. 23, E. 14) with genitalia slide, Aristóbulo del Valle (Misiones), 28 Feb 1951, Duret (CMPHM). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

78. Culex (Mel.) orfilai Duret, 1953. TYPE: Holotype ♂ (D.O 69, E. 20) with genitalia slide, Iguazú, Villa Tacuara (Misiones), 21 Nov 1951, Duret (CMPHM). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

79. Culex (Mel.) pavlovskyi Casal & García, 1967. TYPE: Holotype ♂ with genitalia slide (660331), Aeropuerto de Cambá Punta, near Corrientes (Corrientes), 4 Mar 1966, O. H. Casal (INM). BIONOMICS: Adults taken at a lighted window. [Larvae probably in permanent or semipermanent ground waters.]

80. Culex oblita (Lynch Arribáizaga, 1891) [NEW COMBINATION; NOMEN DUBIUM]. TYPE: Holotype ♂ [only a leg and a wing remain], Navarro, near Arroyo de las Saladas (Buenos Aires), Mar 1884 [F. Lynch] (BA).

81. Sayomyia australis (Shannon & Del Ponte, 1928). TYPE: Lectotype ♀, in good condition, with the following labels, "Ins. Bac. Ent. nota 195/Finca Santa Bárbara, 6.IV.27 Tuc.[umán, Departamento de la Capital]/R.C. Shannon coll & Del Ponte/Chaoborus australis Shannon & Del Ponte" (INM; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: Adults collected at lights. [Larvae probably in permanent or semipermanent still ground waters.]

82. Sayomyia elnorae (Shannon & Del Ponte, 1928). TYPE: ♀, Tres Pozos, near Embarcación (Salta), E. S. Shannon (LU). BIONOMICS: Adults collected at light near a lake. [Larvae probably in lakes and other permanent and semipermanent still ground waters.]

83. Corethrella arborealis Shannon & Del Ponte, 1928 [=appendiculata]. TYPE: Holotype ♂ [(174) and wing slide (389)], Vipos [Tucumán], 4 Mar 1927, E. Del Ponte (INM). BIONOMICS: Holotype bred from pupa from treehole.

84. Corethrella puella Shannon & Del Ponte, 1928. TYPE: Lectotype ♀, in good condition, with the following labels, "Ledesma, Jujuy, 30.3.27/R.C. Shannon coll./Corethrella puella S & DP," the last label by Del Ponte (INM; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: Adults collected in bathroom. [Larvae probably in permanent and semipermanent ground water with dense vegetation.]

85. Corethrella quadrivittata Shannon & Del Ponte, 1928. TYPE: Lectotype

♂, in very good condition, with the following labels, "Tres Pozos, Salta, 20.4.27/Shannon & Shannon./*Corethrella quadrivittata* Shannon y Del Ponte," the last label by Shannon (INM; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: Females taken at light near a lake. Larvae in aquatic vegetation (*Pistia* and others) in lakes.

86. *Lutzomiops davisi* (Shannon & Del Ponte, 1928). TYPE: Lectotype ♀, in fairly good condition, with the following labels, "Ins. Bac. Ent. nota 32-4/Concepción, Tuc.[umán] 4.7.26/R.C. Shannon/390/*Corethrella davisi* Shannon & Del Ponte," the last label by Shannon (INM; PRESENT DESIGNATION by O. H. Casal). BIONOMICS: Larvae in a ground pool with semistagnant water and with vegetation at the margins.

87. *Nothodixa atrovittata* (Edwards, 1930). TYPE: Holotype ♂, Bariloche [San Carlos de Bariloche] (Río Negro), elev. 2450 ft, 25 Oct-1 Dec 1926, F.W. Edwards (BM). BIONOMICS: [Larvae probably in marginal vegetation or flotage in small creeks.]

88. *Nothodixa nitida* (Edwards, 1930). TYPE: Holotype ♂, Bariloche [San Carlos de Bariloche] (Río Negro), elev. 2450 ft, 25 Oct-1 Dec 1926, F.W. Edwards (BM). BIONOMICS: [Larvae probably in marginal vegetation or flotage in small creeks.]

89. *Dixella argentina* (Alexander, 1920). TYPE: Holotype ♂, La Granja, Alta Gracia (Córdoba), 1-8 Apr 1920, Charles Bruch (A). BIONOMICS: [Larvae probably in various types of permanent and semipermanent ground waters, especially at margins of small streams.]

List of Localities

BUENOS AIRES

[Locality not specified]: 38. *Psorophora* (P.) *lynchi*; 44. *Psorophora* (J.) *bruchi*; 48. *Aedes* (O.) *lynchii*.

Baradero: 1. *Anopheles* (A.) *annulipalpis*; 6. *Anopheles* (N.) *albitarsis*; 37. *Aedeomyia squamipennis*; 63. *Culex* (C.) *dolosus*.

Chacabuco: 63. *Culex* (C.) *dolosus*.

Las Conchas: 63. *Culex* (C.) *dolosus*.

Luján (Río): 34. *Uranotaenia pulcherrima*.

Navarro: 28. *Coquillettidia* (R.) *fasciolata*; 54. *Aedes* (O.) *confirmatus* (banks of Río Salado); 63. *Culex* (C.) *dolosus*.

Otamendi (Ingeniero Rómulo) (Canal 6 and Paraná de las Palmas, Estación Agropecuaria Delta de I. N. T. A.): 62. *Culex* (C.) *castroi*; 65. *Culex* (C.) *eduardoi*; *Culex* (C.) *hepperi*.

Paraná, Islas del (Tuyuparé, a brook in the delta of the Paraná): 18. *Trichoprosopon* (R.) *paranensis*; 22. *Wyeomyia* (M.) *leontinae*; 42. *Psorophora* (J.) *centrale*.

San Isidro: 49. *Aedes* (O.) *tapinops*; 61. *Culex* (C.) *brethesi*; 64. *Culex* (C.) *bonariensis*; 75. *Culex* (Mel.) *intrincatus* (lowlands).

Tigre: 32. *Uranotaenia nataliae* (Río Las Conchas).

Zárate: 63. *Culex* (C.) *dolosus*.

CHACO

[Locality not specified]: 25. *Phoniomyia mueblensi*.

Resistencia: 31. *Uranotaenia monilis*; 35. *Uranotaenia urania*.

CORDOBA

Achiras: 68. Culex (C.) lahillei.

La Granja, Alta Gracia: 89. Dixella argentina.

Primero (Río): 70. Culex (C.) autumnalis.

CORRIENTES

[Locality not specified]: 10. Anopheles (N.) bachmanni.

Corrientes: 79. Culex (Mel.) pavlovskyi (Aeropuerto de Cambá Punta).

ENTRE RIOS

[Locality not specified]: 10. Anopheles (N.) bachmanni.

FORMOSA

[Locality not specified]: 10. Anopheles (N.) bachmanni; 16. Toxorhynchites (L.) separatus; 17. Toxorhynchites (L.) lynchi; 30. Uranotaenia lanei; 39. Psorophora (P.) holmbergii; 45. Psorophora (G.) confinnis.

San Jose: 21. Wyeomyia (Dav.) monoleua.

JUJUY

[Locality not specified]: 56. Haemagogus (S.) spegazzinii; 60. Culex (C.) interfor (on train between Tucumán and Jujuy).

Ledesma: 24. Wyeomyia (D.) typharum; 29. Coquillettidia (R.) araozi; 33. Uranotaenia capitis; 84. Corethrella puella (Cañitas Viejo).

San Pedro: 52. Aedes (O.) patersoni; 53. Aedes (O.) raymondi; 58. Culex (Lutzia) patersoni; 69. Culex (C.) maxi.

Santa Clara: 27. Sabethes (S.) neivai.

Zapla: 19. Wyeomyia (N.) lateralis.

MENDOZA

Monte Comán: 72. Culex (All.) tramazayguesi.

MISIONES

[Locality not specified, probably Cataratas del Iguazú]: 50. Aedes (O.) iguazu.

Aristóbulo del Valle: 77. Culex (Mel.) misionensis.

Bernardo de Irigoyen: 74. Culex (Mel.) bejaranoi.

Cataratas: 23. Wyeomyia (D.) belkini (20 km west of).

Cerro Azúl, Arroyo San Juan: 73. Culex (Mel.) aliciae.

Corpus, San Ignacio: 2. Anopheles (A.) holmbergi.

Iguazú (Cataratas del): 26. Limatus exhibitor.

Iguazú, Villa Tacuara: 78. Culex (Mel.) orfilai.

Puerto Iguazú: 13. Toxorhynchites (L.) cavalierii (50 m from Hostería Rufino).

San Pedro: 59. Culex (C.) ameliae (10 km west of, on San Pedro-El Dorado road).

RIO NEGRO

San Carlos de Bariloche, 2450 ft: 87. Nothodixa atrovittata; 88. Nothodixa nitida.

SALTA

[Locality not specified]: 60. Culex (C.) interfor (on train between Tucumán and Jujuy).

Campo Santo de Salta: 71. Culex (C.) saltanensis.

Piquirenda: 66. Culex (C.) fernandezi.

Reserva Nacional "Finca del Rey," Departamento de Anta: 47. Aedes (O.) meprai.

Salvador Mazza (Pocitos), Departamento General San Martín: 55. Haemagogus (S.) petrocchiai.

San Lorenzo (Quebrada de), near Salta: 51. Aedes (O.) araozi.

Tres Pozos, near Embarcación: 12. Anopheles (N.) davisi; 36. Uranotaenia elnora; 43. Psorophora (J.) chaquensis; 46. Psorophora (G.) pauli; 82. Sayomyia elnora; 85. Corethrella quadrivittata.

Vespucio: 76. Culex (Mel.) martinezi (km 34 of Vespucio-San Pedrito road).

SANTA FE

Tapenaga (Río), Colonia Florencia, Gran Chaco: 40. Psorophora (P.) agogylia; 41. Psorophora (P.) stigmatophora.

TUCUMAN

[Locality not specified]: 3. Anopheles (A.) argentinus; 5. Anopheles (A.) patersoni; 7. Anopheles (N.) rooti; 8. Anopheles (N.) evansae; 14. Toxorhynchites (L.) tucumanus; 60. Culex (C.) interfor (on train between Tucumán and Jujuy).

Concepción: 86. Lutzomiops davisi (on road 5 km W).

Lules: 15. Toxorhynchites (L.) arborealis.

Monteros: 9. Anopheles (N.) clarki.

Raco: 20. Wyeomyia (Dav.) petrocchiai.

Salí (Río): 4. Anopheles (A.) tucumanus.

Santa Bárbara (Finca), Departamento de la Capital: 11. Anopheles (N.) perezi; 81. Sayomyia australis.

Vipos: 57. Haemagogus (S.) uriartei; 83. Corethrella arborealis.

BOLIVIA

List of Species

1. Anopheles (Kerteszia) boliviensis Theobald, 1905. TYPE: Holotype ♀, Songo [Zongo] (La Paz), date not specified, M. Biró (BM). BIONOMICS: [Larvae probably in leaf axils of bromeliads.]

2. Toxorhynchites (Ankylorhynchus) hexacis (Martini, 1931). TYPE: Holotype ♀, Yungas de Coroico, Nor Yungas (La Paz), elev. 1000 m (NE). BIONOMICS: [Larvae probably in treeholes or leaf axils.]

3. Trichoprosopon (Ctenogoeldia) magnum (Theobald, 1905). TYPE: Holotype ♀, San Antonio [de Mapiri] (La Paz), M. Biró (HNM). BIONOMICS: [Larvae probably in leaf axils and flower bracts of Calathea or other Marantaceae.]

4. Mansonia (M.) fonsecai (Pinto, 1932) [= indubitans]. TYPE: Holotype ♀ (160), Los Naranjos [Naranjo] (Santa Cruz), 23 Feb 1925, O. da Fonseca (IOC). BIONOMICS: [Larvae probably attached to floating vegetation (Pistia) in ponds or lakes.]

5. Coquillettidia (Rhynchotaenia) nitens (Cerqueira, 1943). TYPE: Holotype ♀, Puerto Suárez, Chiquitos (Santa Cruz), July 1939 (IOC). BIONOMICS: [Larvae probably on rootlets of grasses and other herbaceous vegetation in mud or fine sediment in very shallow water on margins of swamps, ponds or lakes.]

6. *Orthopodomyia bacigalupoi* Martínez & Prosen, 1958 [=fascipes]. TYPE: Holotype ♂, Tacú, Buenavista, Ichilo (Santa Cruz), Apr 1955, A. Martínez and A. F. Prosen (BA). BIONOMICS: Larvae in treeholes.

7. *Psorophora* (*Janthinosoma*) *circumflava* Cerqueira, 1943. TYPE: Holotype ♀, Axiamas, Caupolican (La Paz), Dec 1941 (IOC). BIONOMICS: [Larvae probably in temporary ground pools or overflows of ponds or streams.]

8. *Psorophora* (*J.*) *melanota* Cerqueira, 1943. TYPE: Holotype ♂, Riberalta, Terr. de Colonias (El Beni), Dec 1939 (IOC). BIONOMICS: [Larvae probably in temporary ground pools or overflows of ponds or streams.]

9. *Psorophora* (*Grabhamia*) *chiquitana* Pinto, 1932 [=confinnis]. TYPE: Holotype ♀ (163), Los Naranjos [Naranjo] (Santa Cruz), 1925, O. da Fonseca (IOC). BIONOMICS: [Larvae probably in temporary ground pools or overflows of ponds or streams.]

10. *Psorophora* (*G.*) *dimidiata* Cerqueira, 1943. TYPE: Holotype ♂, Lagunillas, Valle Grande (Santa Cruz), Feb 1940 (IOC). BIONOMICS: [Larvae probably in temporary ground pools or overflows of ponds or streams.]

11. *Aedes* (*Ochlerotatus*) *bejaranoi* Martínez, Carcavallo & Prosen, 1960. TYPE: Holotype ♂, Yungas del Palmar, between km 90 and 110 on road from Cochabamba to Villa Tunari [San Antonio], Chapare (Cochabamba), elev. 3000-3900 m, Feb 1959, A. Martínez (BA). BIONOMICS: Larvae in pools of very cold, slowly flowing water and with dense vegetation and abundant filamentous algae. Adults of both sexes resting in vegetation on margins of pools.

12. *Aedes* (*O.*) *oroecetor* Martini, 1931 [=milleri]. TYPE: Lectotype ♂ with associated genitalia slide, Sorata (La Paz), elev. 2300 m (BM; designation of Mattingly, 1955:29). BIONOMICS: [Larvae probably in shaded stream bed pools with organic debris and surrounded by vegetation.]

13. *Aedes* (*Howardina*) *aurivittatus* Cerqueira, 1943. TYPE: Holotype ♀, Pampa Grande, Florida (Santa Cruz), Feb 1940 (IOC). BIONOMICS: [Larvae probably in leaf axils of bromeliads, possibly in treeholes.]

14. *Aedes* (*H.*) *delpontei* Martínez & Prosen, 1955. TYPE: Holotype ♂, between km 125 (Limbo, elev. 2000 m) and km 145 (Locotal, elev. 1200 m) on road from Cochabamba to Villa Tunari [San Antonio], Chapare (Cochabamba), Jan 1949, Feb 1952 or Nov 1953, A. Martínez and A. F. Prosen (BA). BIONOMICS: [Larvae probably in leaf axils of bromeliads, possibly in treeholes.]

15. *Aedes* (*H.*) *vanemdeni* Martini, 1931. TYPE: Lectotype ♂, Yungas de Coroico, Nor Yungas (La Paz), elev. 1000 m (BM; designation of Mattingly, 1955:31). BIONOMICS: [Larvae probably in leaf axils of bromeliads, possibly in treeholes.]

16. *Haemagogus* (*Stegoconops*) *lindneri* Martini, 1931 [=speggazzinii or urartei]. TYPE: Holotype ♀, [?San José de] Chiquitos (Santa Cruz), Oct 1926 1926 (SMNS). BIONOMICS: [Larvae probably in treeholes.]

17. *Culex* (*C.*) *alticola* Martini, 1931. TYPE: Lectotype ♂, Serata [Sorata] (La Paz), elev. 2300 m, 19 Dec 1902 (BM; designation of Mattingly, 1955:31). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

18. *Culex* (*C.*) *bidens* Dyar, 1922. TYPE: Lectotype ♂ with genitalia slide (1687), Rosario, near Lago Rogagua (El Beni), Nov 1921, W. M. Mann (USNM, 25760; designation of Stone and Knight, 1957a:47). BIONOMICS: [Larvae probably in permanent and semipermanent ground waters.] Adults probably collected in forest islands in generally open country.

19. *Edwardsops boliviensis* Lane & Heredia, 1956. TYPE: Holotype ♀, El Paylon [El Pailon] (Santa Cruz), 5-6 Feb 1955, Travassos, Barros and Albuquerque (FH). BIONOMICS: [Larvae probably in permanent or semipermanent ground pools, possibly in treeholes.]

List of Localities

BENI (EL)

Riberalta: 8. Psorophora (J.) melanota.

Rosario, near Lago Rogagua: 18. Culex (C.) bidens.

San Antonio: (See under LA PAZ).

COCHABAMBA

Chapare Prov.; road from Cochabamba to Villa Tunari (San Antonio): 11. Aedes (O.) bejaranoi (Yungas del Palmar, between km 90 and 110; elev. 3000-3900 m); 14. Aedes (H.) delpontei (between km 125, elev. 2000 m, and km 145, elev. 1200 m).

LA PAZ

Axiamas, Caupolican Prov.: 7. Psorophora (J.) circumflava.

Coroico (Yungas de) elev. 1000 m, Nor Yungas Prov.: 2. Toxorhynchites (A.) hexacis; 15. Aedes (H.) vanemdeni.

San Antonio de Mapiri: 3. Trichoprosopon (Ctenogoeldia) magnum.

Sorata: 12. Aedes (O.) oroecetor; 17. Culex (C.) alticola.

Zongo (Songo): 1. Anopheles (K.) boliviensis.

SANTA CRUZ

Buenavista (Tacú), Ichilo Prov.: 6. Orthopodomyia bacigalupoi.

Chiquitos (?San José de), Agua retirada, Chiquitos Prov.: 16. Haemagogus (S.) lindneri.

Lagunillas, Valle Grande Prov.: 6. Psorophora (G.) dimidiata.

Naranjo (Los Naranjos): 4. Mansonia (M.) fonsecai; 9. Psorophora (G.) chiquitana.

Pailón (El): 19. Edwardsops boliviensis.

Pampa Grande, Flórida Prov.: 13. Aedes (H.) aurivittatus.

Puerto Suárez, Chiquitos Prov.: 5. Mansonia nitens.

CHILE

List of Species

1. Anopheles (A.) neghmei Mann, 1950 [ssp. of pseudopunctipennis]. TYPE: Holotype ♂, Quebrada de Miñemiñe (Tarapacá), elev. 1800 m, Feb-Mar or June 1946, G. Mann F. (Inst. Biol. "Juan Noe," Santiago, A-1). BIONOMICS: Larvae in natural and artificial ground waters.

2. Anopheles (A.) noei Mann, 1950 [ssp. of pseudopunctipennis]. TYPE: Holotype ♂, Oasis of Suca (Tarapacá), elev. 1330 m, Feb-Mar or June 1946, G. Mann F. (Inst. Biol. "Juan Noe," Santiago, A-32). BIONOMICS: Larvae primarily in irrigation waters.

3. Anopheles (Nyssorhynchus) pictipennis Philippi, 1865. TYPE: 2♂; Santiago (Santiago), July 1859; Aconcagua province, Sept 1863 (NE). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

4. Anopheles (N.) bigotii Theobald, 1901 [= pictipennis]. TYPE: Holotype ♀, locality not specified, 1894, J.M.F. Bigot (NE). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

5. Anopheles (N.) variegatus (E. Blanchard, 1852); chilensis (R. Blan-

chard, 1905), nom. nov. [=pictipennis]. TYPE: Lectotype ♀, Arquero [Arqueros?] (MNHP; designation of Belkin, 1968:10). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

6. Psorophora marmorata (Philippi, 1865) [identity doubtful]. TYPE: 2 ♂, 1 ♀, locality not specified (NE). BIONOMICS: [Larvae probably in ground pools.]

7. Aedes (Ochlerotatus) flavipes (Macquart, 1838) [=?albifasciatus]. TYPE: Holotype ♀, Concepción (Concepción), no other data (MNHP). BIONOMICS: [Larvae probably in temporary ground pools or flooded margins of ponds or streams.]

8. Aedes (O.) annuliferus (E. Blanchard, 1852) [=?albifasciatus]. TYPE: Lectotype ♀, probably from vicinity of Coquimbo or Illapel (Coquimbo) (MNHP; designation of Belkin, 1968:4). BIONOMICS: [Larvae probably in temporary ground pools or flooded margins of ponds or streams.]

9. Aedes (O.) vittatus (Philippi, 1865); philipii Dyar, 1924, new name [=?albifasciatus]. TYPE: 2 ♀, Santiago (Santiago), no other data (NE). BIONOMICS: [Larvae probably in temporary ground pools or flooded margins of ponds or streams.]

10. Aedes (O.) colonarius Dyar, 1924 [=?albifasciatus]. TYPE: Holotype ♀, Azapa Valley (Tarapacá), June 1912, C.E. Porter (USNM). BIONOMICS: [Larvae probably in temporary ground pools or flooded margins of streams.]

11. Culex (C.) annuliventris (E. Blanchard, 1852) [A distinct species]. TYPE: Lectotype ♂, possibly from Valdivia (Valdivia) (MNHP; designation of Belkin, 1968:13). BIONOMICS: [Larvae in permanent or semipermanent ground waters.]

12. Culex (C.) apicinus Philippi, 1865. TYPE: Adult, near Santiago (Santiago), no other data (NE). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters, ponds or streams.]

13. Culex (C.) articularis Philippi, 1865. TYPE: Original material from near Corral (Valdivia) all lost (NE); neotype ♂, Casa Pangué (Llanquihue), Dec 1926, R. and E. Shannon (USNM, RB 62 #554; designation of Bram, 1967:30). BIONOMICS: [Larvae in permanent or semipermanent ground waters.]

14. Culex (C.) serotinus Philippi, 1865 [=pipiens complex]. TYPE: ♂, ♀, Santiago (Santiago) and Valdivia (Valdivia), no other data (NE). BIONOMICS: [Larvae probably in ground waters contaminated with domestic wastes or in large artificial containers.]

15. Nothodixa chilensis (Alexander, 1913). TYPE: Holotype ♂, Concepción (Concepción), 23 Aug 1904, P. Herbst (NE). BIONOMICS: [Larvae probably in vegetation or flotage on margins of streams, rivulets, seepages and springs.]

16. Nothodixa ensifera (Edwards, 1930). TYPE: Holotype ♂, Casa Pangué (Llanquihue), elev. about 1000 ft, 4-10 Dec 1926, F.W. Edwards (BM). BIONOMICS: [Larvae probably in vegetation or flotage on margins of streams, rivulets, seepages and springs.]

List of Localities

[NOT SPECIFIED]

Locality and province not specified, probably near Santiago or Valparaíso:
4. Anopheles (N.) bigotii; 6. Psorophora marmorata.

ACONCAGUA

[Locality not specified]: 3. Anopheles (N.) pictipennis (also Santiago).

CONCEPCION

Concepción: 7. Aedes (O.) flavipes; 15. Nothodixa chilensis.

COQUIMBO

Arqueros: 5. Anopheles (N.) variegatus.

Coquimbo: 8. Aedes (O.) annuliferus (also Illapel).

Illapel: 8. Aedes (O.) annuliferus (also Coquimbo).

LLANQUIHUE

Casa Pangué, frontier station on Chilean side of Rosales Pass, altitude of house about 1000 ft: 13. Culex (C.) articularis; 16. Nothodixa ensifera.

SANTIAGO

Santiago: 3. Anopheles (N.) pictipennis (also Aconcagua Prov.); 9. Aedes (O.) vittatus; 14. Culex (C.) serotinus (also Valdivia).

See also [NOT SPECIFIED].

TARAPACA

Azapa Valley: 10. Aedes (O.) colonarius.

Miñemiñe, Quebrada de: 1. Anopheles (A.) neghmei.

Suca, Oasis of: 2. Anopheles (A.) noei.

VALDIVIA

Corral: 13. Culex (C.) articularis.

Valdivia: 11. Culex (C.) annuliventris; 14. Culex (C.) serotinus (also Santiago).

PARAGUAY

List of Species

1. Phoniomyia fuscipes (Edwards, 1922). TYPE: Lectotype ♀, unspecified locality in Paraguay, probably Asunción (Asunción), Fiebrig (BM; designation of Belkin, 1968:24). BIONOMICS: [Larvae probably in leaf axils of bromeliads.]

2. Psorophora (P.) pallescens Edwards, 1922. TYPE: Lectotype ♂ with attached genitalia mount, unspecified locality in Paraguay, probably Asunción (Asunción), Fiebrig (BM; designation of Belkin, 1968:28). BIONOMICS: [Larvae probably in temporary ground pools or overflows of ponds and streams.]

3. Psorophora (Janthinosoma) purpurascens Edwards, 1922 [=cyanescens]. TYPE: Holotype ♀, locality and date not specified, probably Asunción (Asunción), Fiebrig (HNM). BIONOMICS: [Larvae probably in sunlit temporary ground pools.]

4. Psorophora (J.) fiebrigi Edwards, 1922 [=ferox]. TYPE: Lectotype ♂ with attached genitalia mount, unspecified locality in Paraguay, probably Asunción (Asunción), Fiebrig (BM; designation of Belkin, 1968:26). BIONOMICS: [Larvae probably in temporary ground pools in wooded or shaded areas.]

5. Psorophora (J.) paraguayensis (Strickland, 1911) [=varipes]. TYPE: Holotype ♀, Puerto Max (Boquerón), Jan-Apr 1905, Vezényi (NE). BIONOMICS: [Larvae probably in temporary pools in wooded or shaded areas.]

6. Psorophora (Grabhamia) varinervis Edwards, 1922. TYPE: Holotype ♀, locality and date not specified, probably Asunción (Asunción), Fiebrig (HNM).

BIONOMICS: [Larvae probably in temporary ground pools or overflows of ponds and streams.]

7. Aedes (Ochlerotatus) stigmaticus Edwards, 1922. TYPE: Lectotype ♀, Asunción (Asunción), 1904, Vezényi (BM; designation of Belkin, 1968:7). BIONOMICS: [Larvae probably in temporary ground pools or overflows of ponds and streams.]

List of Localities

ASUNCION

[Locality not specified, probably vicinity of Asunción]: 1. Phoniomyia fuscipes; 2. Psorophora (P.) pallescens; 3. Psorophora (J.) purpurascens; 4. Psorophora (J.) fiebrigi; 6. Psorophora (G.) varinervis.

Asunción: 7. Aedes (O.) stigmaticus.

BOQUERON

Puerto Max: 5. Psorophora (J.) paraguayensis.

PERU

List of Species

1. Anopheles (Stethomyia) acanthotorynus Komp, 1937. TYPE: Holotype ♂ with genitalia slide, Iquitos (Loreto), Apr 1931, R. C. Shannon (USNM, 52020). BIONOMICS: [Larvae probably in deeply shaded stream bed pools.]

2. Anopheles (A.) peruvianus Tamayo, 1907 [=pseudopunctipennis]. TYPE: ♂, ♀, Huacachina (Ica), San Pedro de Lloc (La Libertad), Lima, summer and fall, Chanchamayo (LU). BIONOMICS: [Larvae probably in various small, sunlit, permanent and semipermanent ground waters with algae.]

3. Trichoprosopon (T.) subsplendens (Martini, 1931) [=digitatum]. TYPE: Holotype ♀, Pt. Bermudas [Bermudez], Pichis [Río] (Pasco), 10/12.03 (NE). BIONOMICS: [Larvae probably in treeholes, cut bamboo or plant parts on the ground.]

4. Trichoprosopon (Runchomyia) hyperleucum (Martini, 1931). TYPE: Holotype ♀, Urubamba River (Cuzco) (NE). BIONOMICS: [Larvae probably in treeholes, cut bamboo, plant parts on the ground, or in the leaf axils and/or flower bracts of Araceae, Marantaceae, Musaceae or bromeliads.]

5. Aedes (Ochlerotatus) epinolus Dyar & Knab, 1914 [=taeniorhynchus]. TYPE: Lectotype ♀, Ventanillas (Cajamarca), 4 Feb 1914, C. H. T. Townsend (USNM, 18362; designation of Stone and Knight, 1956a:217). BIONOMICS: [Larvae probably in coastal saltmarshes or freshwater pools near the sea.]

6. Haemagogus (Stegoconops) obscurescens Martini, 1931 [=anastasionis]. TYPE: Lectotype ♀, Ucayali River (Loreto) (BM; designation of Mattingly, 1955:28). BIONOMICS: [Larvae probably in treeholes or cut bamboo.]

7. Culex (C.) debilis (Dyar & Knab, 1914) [=apicinus]. TYPE: Lectotype ♂ with genitalia and 3 legs on slides (597, 598), Matucan [Matucana] (Lima), elev. 7300 ft, June-July 1913, C. T. Brues (USNM, 18361; designation of Stone and Knight, 1957a:47). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

8. Culex (C.) escomeli Brèthes, 1920 [=apicinus]. TYPE: ♂, ♀, Arequipa (BA). BIONOMICS: [Probably as for 7. debilis.]

9. Culex (C.) archegus Dyar, 1929. TYPE: Holotype ♂, Tarma (Junín), elev. 10,000 ft, 13 July 1928, R.C. Shannon (USNM). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

10. Culex (C.) diplophyllum Dyar, 1929. TYPE: Lectotype ♂ with genitalia slide (2398), Verrugas Canyon (Lima), 5 Apr 1928, R.C. Shannon (USNM; designation of Stone and Knight, 1957a:47). BIONOMICS: [Larvae probably in permanent or semipermanent ground waters.]

11. Culex (C.) raymondii Tamayo, 1907 [= pipiens quinquefasciatus]. TYPE: ♂, ♀, larva, pupa, Huacachina (Ica) (LU). BIONOMICS: [Larvae probably in ground waters contaminated with domestic wastes or in large artificial containers.]

12. Corethrella inca Lane, 1939 [= ananacola]. TYPE: Holotype ♀, Iquitos (Loreto), Mar-Apr 1931, R.C. Shannon (FH). BIONOMICS: [Larvae probably in leaf axils of bromeliads, possibly Ananas magdalenae.]

13. Corethrella maculata Lane, 1939. TYPE: Holotype ♂, Iquitos (Loreto), Mar-Apr 1931, R.C. Shannon (FH). BIONOMICS: [Larvae probably in ground waters, possibly in leaf axils or treeholes.]

14. Lutzomiops peruviana (Lane, 1939). TYPE: Holotype ♀, Iquitos (Loreto), Mar-Apr 1931, R.C. Shannon (FH). BIONOMICS: [Larvae probably in swamps.]

15. Lutzomiops shannoni (Lane, 1939). TYPE: Holotype ♂, Iquitos (Loreto), Mar-Apr 1931, R.C. Shannon (USNM). BIONOMICS: Larvae in a swamp.

16. Dixella andeana (Lane, 1942). TYPE: Holotype ♂, Iquitos (Loreto), Mar-Apr 1931, R.C. Shannon (USNM). BIONOMICS: [Larvae probably on margins of small streams or permanent or semipermanent ground pools.]

17. Dixella peruviana (Edwards, 1931). TYPE: Holotype ♂, Verrugas (Lima), 5 May 1928, R.C. Shannon (BM). BIONOMICS: [Larvae probably on margins of small streams or springs.]

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LA LIBERTAD

San Pedro de Lloc: 2. Anopheles (A.) peruvianus (also Huacachina (Ica) and Lima).

LIMA

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1. Psorophora (Grabhamia) leucocnemis Martini, 1931 [?= varinervis].
TYPE: Holotype ♀, Montevideo (Montevideo), 19 Mar 1927, Vogelsang coll. 8846 (BM). BIONOMICS: [Larvae probably in temporary ground pools or overflows of ponds or streams.]

REFERENCES CITED

Belkin, John N.

1968. Mosquito Studies (Diptera, Culicidae). IX. The type specimens of New World mosquitoes in European museums. Amer. Entomol. Inst., Contrib. 3(4). 69 p.

Belkin, John N., R. X. Schick and S. J. Heinemann

1965. Mosquito Studies (Diptera, Culicidae). V. Mosquitoes originally described from Middle America. Amer. Entomol. Inst., Contrib. 1(5): 1-95.

1966. Mosquito Studies (Diptera, Culicidae). VI. Mosquitoes originally described from North America. Amer. Entomol. Inst., Contrib. 1(6): 1-39.

Bram, Ralph A.

1967. Classification of Culex subgenus Culex in the New World. U. S. Nat. Mus., Proc. 120:1-122.

Castro, Manuel and M. Bressanello

1952. Revisión de las especies de Taeniorhynchus (Rhyncotaenia) (Dipt. Cul.). Rev. Brasil. Biol., Rio de Janeiro 12:229-246.

García, Miguel and R. A. Ronderos

(1962) 1963. Sobre la validez de Aedes (Ochlerotatus) patersoni Shannon y del Ponte, 1927 (Diptera-Culicidae). Soc. Entomol. Argent., Rev., Buenos Aires 25:29-33.

Peters, T. Michael

1968. Mosquito Studies (Diptera, Culicidae). X. Dixinae originally described

from North America. Amer. Entomol. Inst., Contrib. 4(1):1-7.

Stone, Alan and K. L. Knight

1955. Type specimens of mosquitoes in the United States National Museum: I. The genera Armigeres, Psorophora and Haemagogus (Diptera, Culicidae). Wash. Acad. Sci., J. 45:282-289.

1956. Type specimens of mosquitoes in the United States National Museum: III. The genera Anopheles and Chagasia (Diptera, Culicidae). Wash. Acad. Sci., J. 46:276-280.

1957a. Type specimens of mosquitoes in the United States National Museum: IV. The genus Culex (Diptera, Culicidae). Wash. Acad. Sci., J. 47:117-126.

1957b. Type specimens of mosquitoes in the United States National Museum: V. The Sabethini (Diptera, Culicidae). Wash. Acad. Sci., J. 47:117-126.

1957c. Type specimens of mosquitoes in the United States National Museum: VI, Miscellaneous genera, addenda, and summary. Wash. Acad. Sci., J. 47:196-202.

Umana, A. C., R. L. Heredia and J. C. Siquot

1959. Estudios sobre el Anopheles (N.) albitarsis en la Argentina (Nota previa). Primeras Jornadas Entomoepidemiológicas Argentinas, Buenos Aires, part 2, p. 609-618.

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MOSQUITO STUDIES (Diptera, Culicidae)

XII. A revision of the Neotropical subgenus *Howardina* of
Aedes. By O. G. W. Berlin



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MOSQUITO STUDIES (Diptera, Culicidae)

XII. A REVISION OF THE NEOTROPICAL SUBGENUS

HOWARDINA OF AEDES¹

By

O.G.W. Berlin²

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INTRODUCTION

The exclusively Neotropical subgenus *Howardina* has been recognized as a distinct entity in the widespread genus *Aedes* since Dyar's classification of the American species of the genus (Dyar 1920:103-106) but no attempt has been made to date to develop an internal classification of this subgenus. Nearly all species assigned to *Howardina* have been characterized entirely on the pattern of ornamentation of the adults. The immature stages were largely unknown. In recent years, considerable associated reared material has accumulated and it is now possible to attempt a comprehensive revision of the subgenus based on all stages.

The taxonomic history of *Howardina* is brief and relatively simple except for confusion with other generic group taxa (*Finlaya*, *Haemagogus*, *Stegomyia*, etc.) which need not be detailed here. *Howardina* was proposed by Theobald (1903:287) as a distinct genus with 2 included species, *walkeri* and *greenii*, and with the following definition: "Head clothed with flat and narrow curved scales, the latter forming a median area as in *Aedes*. Scutellum with narrow curved scales; the midlobe with four posterior border-bristles. Wings with lateral vein-scales large for the size of the wings, long, rather thin, the median vein-scales small. Palpi of the ♀ minute, four-jointed; the penultimate joint long, longer than the two basal ones; apical joint very minute. ♂ unknown. All small species, and with ornamented thorax." Dyar (1905:44) selected *walkeri* as the type species of *Howardina*. Coquillett (1906:312) recognized the importance of the simple claws, a character mentioned in the original description of *walkeri*. By 1910 Theobald recognized 7 species in the genus, described by himself and by Grabham, but 3 of these were subsequently removed to the genus (later subgenus) *Finlaya*. Howard, Dyar and Knab (1912a:65,70) synonymized *Howardina* with *Aedes* but Dyar (1920:103) elevated it to subgeneric rank within *Aedes* on the basis of male genitalic characters (rudimentary claspette). All other contributions between 1910 and 1932 were merely descriptions of individual species. Edwards (1932:155-156) in his classic revision of the mosquitoes of the world listed 13 species in the subgenus *Howardina* and gave the following brief diagnosis which has been followed by all authors to the present: "most closely related to *Finlaya*, from which it differs chiefly in the simple claws of the ♀; less prominent eighth sternite of ♀ abdomen; and less developed claspette of ♂ hypopygium, the stem being very short and the appendage bristle-like. Vertex in all species with a median stripe of narrow scales reaching forward to eyes; scutellar scales narrow. Thorax conspicuously ornamented with white or golden lines. Larva.- Similar to that of *Finlaya*; a more or less distinct small chitinous plate present on each side of the ventral brush." Subsequent to Edwards' revision more confusion than progress has been accomplished, particularly in erroneous identifications of species. In the world catalog of mosquitoes (Stone, Knight and Starcke 1959:175-176) 16 species were recognized on the basis of published records.

Included in Edwards' (1932:155-156) list of species of *Howardina* were *dominicii* and *whitmorei* for which Komp (1936:71) subsequently erected the subgenus *Soperia*, with *dominicii* as the type species. Unfortunately Komp misidentified *dominicii* which in reality is conspecific with *sexlineatus* in the subgenus *Howardina*. Komp based the new subgenus primarily on the complete absence of a claspette in the male genitalia. *Soperia* has been considered as a distinct subgenus to the present and contained 3 species in the world catalog (Stone, Knight and Starcke 1959:173), one of which, *tracei*, was synonymized with *busckii* in the subgenus *Howardina* by Belkin, Schick and Heinemann (1965:33).

In the present study only the subgenus *Howardina* is recognized; the species formerly placed in *Soperia* of authors form a distinct group included in the Sexlineatus Section, 1 of 3 primary divisions of *Howardina*. A total of 35 species is now recognized in the subgenus: 5 species in 1 group in the Fulvithorax Section; 11 species in 5 groups in the Walkeri Section; and 19 species in 6 groups in the Sexlineatus Section.

I wish to express my gratitude to Dr. John N. Belkin for suggesting this project and directing the study. I am indebted to Dr. Alan Stone of the U.S. National Museum for the loan of material and for information on type specimens; to Dr. P.F. Mattingly for the loan from the British Museum; and to Dr. A. Martinez, Dr. A. Spielman and Dr. A. Diaz Najera for specimens from Argentina, Bahamas and Mexico respectively. I also thank Pedro Galindo, Gorgas Memorial Laboratory, Panama, and Dr. I. Goodbody, Department of Zoology, University of West Indies, Kingston, Jamaica, for the courtesies extended to me during field trips to these countries. Finally I wish to thank Dr. R.X. Schick, Dr. S. Sirivanakarn, Dr. T.J. Zavortink and Miss Sandra Heinemann for the valuable suggestions and assistance and to Miss Sheila Bernstein for the preparation of the final copy for reproduction.

MATERIAL AND METHODS

MATERIAL. This study is based largely on extensive collections of adults and associated immature stages accumulated at the University of California, Los Angeles for the project "Mosquitoes of Middle America" (Belkin, Schick et al, 1965) and also on material from the U.S. National Museum and the British Museum (Nat. Hist.) where most of the types of previously described species are deposited. Additional critical material was obtained specifically for this study in Jamaica in November and December 1966 following the methods of collection and rearing outlined by Belkin, Hogue et al (1965).

For this revision a total of 10,949 specimens were studied, including 1,240 ♂, 3,527 ♀, 2,412 pupae, 3,770 larvae, with 1,796 individual rearings (810 pupal, 645 larval, 341 incomplete).

TAXONOMIC PROCEDURE. The taxonomic methods used in this study are the classical phylogenetic ones, simple in principle but difficult in practice. Following the recognition of species on the basis of a series of constant correlated characters in all stages, the different species were compared minutely and those showing the greatest similarities in all stages were interpreted as members of primary phyletic lines or species groups, called simply Groups here. These groups were compared in turn to establish the more inclusive Sections within the subgenus.

DESCRIPTIONS. The method of presentation, terminology and abbreviations used in the descriptions of taxa in general follow Belkin (1962). A few special terms used for the pattern of ornamentation of adults are explained in the section on taxonomic characters in the following chapter.

ILLUSTRATIONS. All available stages of every species are figured, the larvae and pupae in full and the adults in pertinent details only. Each illustration is based on a topotypic specimen, whenever available, but the character states shown represent the modal condition determined usually from at least 10 topotypic specimens. In the illustrations of the ornamentation of mesonotum and pleuron, dotted lines represent golden or creamy scales and dashed lines denote white or silvery scales.

DISTRIBUTION DATA. In the distribution lists, the arrangement of countries is from north to south and west to east and the localities in each country are listed alphabetically under the major political subdivisions. Included in these lists are all the records of material I have examined as well as published records from the literature which I consider reliable. In these lists, P and L denote whole pupa and larva and p and l, pupal and larval skins respectively.

DEPOSITORIES. The abbreviations used by Stone, Knight and Starcke (1959) for institutions in which types are deposited are followed here to indicate the location of the material studied. To these are added the Institute of Jamaica [IJ] and the Department of Zoology, Los Angeles, California [UCLA]. The bulk of the material will remain at UCLA. The types of all new species described here will be deposited in the U.S. National Museum.

GENERAL CONSIDERATIONS

TAXONOMIC CHARACTERS. The following discussion is limited to external morphological characters. Other important taxonomic characters, ecological and geographical, are discussed below in the sections on Bionomics and Distribution respectively.

In the adults, the most important taxonomic characters pertain to the pattern of ornamentation of the mesonotum. As indicated in the diagnosis of the subgenus, the pattern usually consists of lines of light scales superimposed on a background of dark scales. Each section, each group and most species have a distinctive pattern of ornamentation. It was necessary to develop a special terminology for these light lines as no suitable one was available. This terminology is illustrated in figs. 8 and 9 and explained below. The *acrostichal line* is the single median longitudinal mesonotal line and is developed only in some members of the Fulvithorax Section; it ends in front of the prescutellar space and is more or less distinctly continued caudad as a pair of *lateral prescutellar lines*. The *median prescutellar line* is developed only in the Walkeri Section and is in the median longitudinal position in the "bare" prescutellar space. The *inner dorsocentral lines* are located mesad of the dorsocentral row of bristles in a submedian longitudinal position on each side; these lines reach the scutellum only in the Sexlineatus Section; the posterior parts (prescutellar) of these lines more or less correspond to the lateral prescutellar lines found in some members of the Fulvithorax Section. The *outer dorsocentral lines* are located laterad of the dorsocentral row of bristles in a sublateral longitudinal position; they are represented to a varied degree in all sections and usually reach the lateral lobes of the scutellum in the Walkeri and Sexlineatus Sections. The *lateral marginal lines* border the mesonotum on each side to a varied degree from the anterior promontory to the wing root; they may be broken into one or more prescutal and antealar segments. Transverse diagonal *posterior fossal lines* may connect the lateral marginal to the outer dorsocentral on each side. Longitudinal *supraalar lines* may also be developed and connected to the lateral marginal lines on each side caudad of the scutal angle. In *fulvithorax* and to a lesser extent in *arborealis* of the Fulvithorax Section, the ornamentation is primarily light and may be considered to have been developed by the expansion and fusion of the light lines which are discrete in the other sections, particularly in the Walkeri Section.

Other significant taxonomic features of adult ornamentation are: (1) on the *head*, scaling of the vertex and of the torus and first flagellar segment of the antenna; (2)

scaling of the *paratergite*; (3) distribution of the scales on the *pleuron*, particularly *ppn*, *stp* and *mep*; (4) on the *legs*, light scaling of the foretibia, midfemur and hindfemur, and the distribution and extent of light scales on the tarsal segments.

The comparatively simple male genitalia of *Howardina* show relatively few obvious taxonomic characters; even specific differences are usually subtle and sometimes not apparent. The reduced claspette is more or less characteristically developed in each section and is absent in the Whitmorei Group. Other significant taxonomic characters appear to be: (1) extent of separation of the base of the sidepieces midsternally, (2) width and length of the aedeagus in relation to the proctiger and (3) the shape of the aedeagus in dorsal aspect. Only 3 species (*bahamensis*, *whitmorei* and *pseudodominicii*) have genitalia strikingly differentiated from the others in features of the sidepieces.

The pupae are quite similar in the subgenus but a few characters separating the 3 sections have been noted in: (1) development of cephalothoracic hair 5-C, (2) position of abdominal hair 2-IV-VI and (3) development of abdominal hair 9-VI. On the other hand, reliable group characters within a section have not been found and specific differences are rather subtle and not always reliable.

The 4th-instar larvae show many taxonomic characters at the section and group levels usually concordant with those of adult ornamentation, and many reliable specific differences. Among the important taxonomic characters are: (1) presence or absence of marginal spicules on the anal saddle, (2) comb scales in a single row or in a patch, (3) ventral brush with 5 or 6 pairs of hairs, (4) prothoracic hair 13-P present or absent, (5) presence or absence of integumentary spicules on the thorax and/or abdomen, and (6) numerous features in the development of hairs, particularly on the head.

BIONOMICS. All members of the subgenus, as far as known, are container breeders. Immature stages have been reported from rockholes, treeholes, broken bamboo, plant parts on the ground, leaf axils of bromeliads and aroids, and flower bracts of heliconias. A few species invade artificial containers of various types. Only the Walkeri Section utilizes the full range of breeding habitats; the Fulvithorax Section is apparently restricted to treeholes and broken bamboo and the Sexlineatus Section is known to breed only in bromeliad axils.

In common with other ornamented mosquitoes, species of *Howardina* are apparently largely diurnal in activity (Bates 1944:159-170; 1949:16,61; Carpenter, Galindo and Trapido 1952:163; Trapido, Galindo and Carpenter 1955:530,537,538; Forattini 1965:401-403). To supplement the published information, I made a full 24-hour observation on the biting activity of females near Porus, Manchester, Jamaica at an elevation of approximately 1000 ft, where 4 species of *Howardina* were present. Biting-landing collections were made at hourly intervals at ground level under bromeliad laden trees. As seen in fig.7 there appear to be specific or group differences in activity since *walkeri* shows 2 definite peaks, a higher one in the morning, and members of the Aurites Group show only a moderate afternoon peak.

Although a number of species are known to bite man in forested areas, the definite altitudinal stratification of different species suggests that their natural hosts are a variety of vertebrates characteristic of a particular stratum in the forest. Members of the Quadrivittatus Group have been collected mainly in the forest canopy (Trapido and Galindo 1957:122,123,124,125,131), while members of the Fulvithorax Group are predominantly forest floor biters (Trapido and Galindo 1957:131); members of the Sexlineatus Group (Trapido and Galindo 1957:132) and Whitmorei Group (Bates 1944:166), on the other hand, demonstrate inconsistent behavior.

DISTRIBUTION (fig.1). *Howardina* is strictly a Neotropical taxon, centered in the American Mediterranean region in the sense of Belkin (1962:562). At present its known northern limit is Grand Bahama Island in the east and the Sierra Madre del Sur and the southern end of the Sierra Madre Oriental in Mexico in the west. The southern limit appears to be in northern Argentina along the Andes; the subgenus apparently does not reach the mouth of the La Plata river in the east.

The distributions of the 3 sections are largely complementary. The Walkeri Section is almost entirely confined to the islands of the Caribbean area with only a slight overlap with the other 2 in northern Venezuela and Trinidad. The Fulvithorax Section is found primarily in eastern South America but with a significant overlap with the Sexlineatus Section in southern Central America. The Sexlineatus Section is primarily associated with the mountain regions of Central America and western South America.

SYSTEMATICS AND EVOLUTION. The 35 species recognized in the present study fall into 12 largely well-defined, discrete groups of 1 or more species each. On the basis of morphological similarity the 12 groups form 3 very distinct sections in the subgenus, the Fulvithorax Section with only 1 group (Fulvithorax) of 5 species (1 not named), the Walkeri Section with 5 groups (Walkeri, Aurites, Ioliota, Albonotatus, and Busckii) of 11 species, and the Sexlineatus Section with 6 groups (Quadrivittatus, Sexlineatus, Whitmorei, Allotecnion, Eleanorae and Aurivittatus) of 19 species.

As indicated in the preceding discussions, as well as in the taxonomic treatment of each section, there is practically no overlap in diagnostic morphological characters among the 3 sections, little overlap in distribution, and strong differentiation in the breeding sites between Fulvithorax Section and the Sexlineatus Section. It appears, therefore, that the 3 sections represent 3 old phyletic lines.

In spite of this clear-cut divergence, there is a remarkable basic similarity in all stages in all 3 sections. This is undoubtedly indicative of true affinity and some kind of monophyletic origin. Two general explanations for the development of 3 major phyletic lines in *Howardina* are possible. First, would be serial or independent development of 2 of the sections from the third; this is not plausible because each of the lines has retained primitive features absent in 1 or 2 of the others. Second, would be a tripartite splitting of one ancestral species. This interpretation is supported by the present distributions of the 3 sections and I therefore suggest on this basis that the original stock was divided into 3 segments: (1) one in the Caribbean, giving rise to the Walkeri Section, (2) one in Central America, giving rise to the Sexlineatus Section, and (3) one in northeastern South America, giving rise to the Fulvithorax Section.

Subsequent speciation and evolution have followed different patterns in each section, probably because of different environmental conditions. In the Fulvithorax Section, which occupies primarily eastern South America where relatively few barriers to dispersal have existed, at least in relatively recent geological times, there has been little differentiation and speciation. The Walkeri Section shows typical complex insular speciation of a variety of divergent types, including relict forms. In the rather homogeneous Sexlineatus Section the extensive speciation reflects the barriers and environmental diversity associated with the complex orogenies of the cordilleras of western America.

AFFINITIES. The general similarity between the subgenera *Howardina* and *Finlaya* has been recognized by many culicidologists, notably Edwards (1932:156), and as indicated in the introduction, some species of *Finlaya* were originally included in *Howardina*, primarily on the basis of the ornamentation of the adults. The chief dif-

ferences from *Finlaya* are the untoothed claws and less prominent sternite VIII in the females and the claspette poorly developed or completely absent in the males. In the last feature, *Howardina* shows little difference from the Oriental *dissimilis* subgroup of *Finlaya* (Knight and Marks 1952:516-517). The immature stages of *Howardina* also bear a general resemblance to those of *Finlaya* and are very similar to those of some species of the genus *Haemagogus*, which is also restricted to the Neotropical region and may have evolved from a *Finlaya* stock "through some such species as *A. (F.) leucocelaenus*" (Edwards 1932:178). The following unusual combination of features in the larvae of *Howardina* may be diagnostic for the subgenus: abdominal hair 12-I never developed, hair 9-I always ventrad of hair 7-I, and tubercles of prothoracic hairs 5-7-P usually distinctly joined (except in *Fulvithorax* Section).

Little can be done now to clarify the affinities of *Howardina* chiefly because the immature stages of the majority of annectant groups in the tribe Aedini are very poorly known both in the Old World and the New World. In spite of some apparent slight overlap with the subgenus *Finlaya* and the genus *Haemagogus*, *Howardina* is a very distinct group, and should be retained as a subgenus of *Aedes*.

MEDICAL IMPORTANCE. Little information is available on the medical importance of species of *Howardina*. A few of the more abundant species were investigated in connection with studies on the vectors of jungle yellow fever. Experimental studies with *fulvithorax* showed that while it could be infected with and maintain the virus, it was not able to transmit it naturally through bites (Davis and Shannon 1931; Whitman and Antunes 1937). Similar results were obtained with other species of *Howardina* by Boshell-Manrique and Osorno-Mesa (1944), Bugher, Boshell-Manrique et al (1944) and Aitken (1960). Bates (1949:205) has suggested that the incubation period of this virus in some mosquitoes may be a long one and it is possible that *Howardina* species may transmit the yellow fever virus if the incubation period is prolonged at favorable temperatures. Galindo (1964) reported the isolation of an unidentified virus from *quadrivittatus* in Panama. Since some species of *Howardina*, especially members of the Walkeri Section (Walkeri, Aurites and Busckii Groups), attack man readily and are very abundant, a more thorough investigation of the role of these species as vectors of arboviruses should be made.

TAXONOMIC TREATMENT

Subgenus **HOWARDINA** Theobald

1903.*Howardina* Theobald, 1903:287. TYPE SPECIES: *Culex walkeri* Theobald, 1901, Jamaica; the second of 2 included species, selection of Dyar (1905a:49).

1936.*Soperia* Komp, 1936b:71. TYPE SPECIES: *Aedes dominicii* Rangel and Romero-Sierra, 1907, Venezuela, original designation. **NEW SYNONYMY.**

Aedes (Howardina) of Dyar (1920:10); Bonne and Bonne-Wepster (1925:366); Dyar (1928:103); Shannon (1931:125); Edwards (1932:155); Gerry (1932:40); Lane (1939:98); Anduze (1941:14); Bates (1949:320); Lane (1949:255,261); Del Ponte, Castro and Garcia (1951:231,239); Lane (1953:706); Levi-Castillo (1953:40); Horsfall (1955:471); Martinez and Prosen (1955:21-22); Peyton, Galindo and Blanton (1958:95-100); Stone, Knight and Starcke (1959:173-174); Martinez, Prosen and Carcavallo (1960:25); Belkin (1962:340); Stone (1963:127); Prosen, Carcavallo and Martinez (1964:103); Forattini (1965:397-401); Cova Garcia, Sutil and Rausseo (1966a:in part; 1966b:333); Porter (1967:38); Stone (1967:208).

Aedes (Soperia) of Lane (1939:98); Anduze (1941:14); Senevet and Quievreux (1941:258); Anduze (1943:193; 1947:357); Lane (1953:700); Levi-Castillo (1953:40); Komp (1956:38); Stone, Knight and Starcke (1959:173); Forattini (1965:404,460,462); Cova Garcia, Sutil and Rausseo (1966b:338-339).

Howardina of Blanchard (1905:399,415); Dyar (1905:49); Theobald (1905:21); Theobald and Grabham (1905:7); Coquillett (1906b:16,26); Dyar and Knab (1906b:188); Theobald (1907:21,149,214); Coquillett (1910:553); Theobald (1910:220); Surcouf and Gonzalez-Rincones (1911:102,139-141; 1912:276).

Aedes in part of Howard, Dyar and Knab (1912:65,70; 1917:613); Dyar (1918:71).

FEMALES (fig.16). Small to medium sized ornate species; usually blackish to dark brown with white, silver, creamy, yellowish or golden markings on head, thorax and abdomen and with white basal tarsal markings. *Head*: Eyes distinctly separated between antennae. Decumbent scales predominantly broad and flat; narrow scales usually largely restricted to median longitudinal light stripe of varied width running from lower end of interocular space to occiput; lower end of interocular space always with a tuft of very long outstanding narrow bristlelike striated scales; orbital line of narrow light scales, varied in width and length, frequently developed. Erect scales short, usually forked apically, restricted to occiput or extending on to the disc and sides of vertex. One pair (rarely 2) of interorbital bristles always differentiated; a single row of orbitals, upper usually 4(3-6) pairs, heavier, longer and more closely spaced than lower. Clypeus bare, deep brown to black. Proboscis slender; subequal to or distinctly longer than forefemur; entirely dark scaled; with a few basal bristles. Palpus always short, about 0.15 to 0.2 of proboscis; 5-segmented, segments 1 and 2 ankylozed, segment 5 minute; segments 1 and 5 without scales, remainder entirely or predominantly dark scaled, light scales usually restricted to apex of segment 4. Antenna distinctly shorter than or subequal to proboscis; torus dark brown to black, with light to dark scales always present, sometimes indistinct, usually restricted to mesal surface; flagellar segment 1 only slightly longer than segment 2, always with a few small scales on mesal surface; flagellar segments 2-13 usually with 6 moderate bristles in basal whorls. *Thorax*: Integument dark brown to almost black. Mesonotum usually with a background of short, narrow curved scales auburn to black in color and with a varied pattern of lines of light scales (except in *fulvithorax* and *arborealis* in which light scales predominate) as follows: (1) median acrostichal, (2) inner dorso-central, (3) outer dorsocentral, (4) lateral marginal, (5) prescutal, (6) posterior fossal, (7) supraalar, (8) median prescutellar and (9) lateral prescutellar. Acrostichal bristles usually not developed on disc (present in *busckii*); dorsocentrals, prescutellars and supraalars always present, variously developed; 1 posterior fossal and 1 parascutellar always developed. Median scutellar lobe with 4,5 large marginal bristles and with dark broad flat scales laterally and narrow light scales in varied median longitudinal line; lateral lobe with 3-5 large marginal bristles and usually with narrow scales only. Paratergite bare or with scales. Bristles present on *apn*, *ppn*, *ppl*, *psp*, *stp*, *pra* and upper *mep*; lower *mep* bristles always absent; lowermost *stp* bristles distinctly ventrad of lower margin of *mep*. Pleural scaling dingy white, white or silvery; always present on *apn*, *ppl*, base of *pra*, *stp* and *mep*; *ppn*, *psp*, and *ssp* with or without scales. *Legs*: Coxae with light scales on external surface; trochanters with mesoventral light scales. White or silvery knee spots prominent on midleg and hindleg, slightly indicated on foreleg. Midfemur and hindfemur with or without distal light spot on anterior surface. Tibiae completely or predominantly dark; light scaling either as narrow lines or as patches. Tarsal white rings always basal, usually restricted to proximal segments. Claws simple on all legs but with minute spicules at base of external surface. *Wing*:

Veins usually entirely dark scaled, white scales rarely present on remigium; plume scales restricted to veins R_s , R_{2+3} , R_2 , R_3 and M. *Abdomen*: Tergite I with numerous scales; laterotergite with large white or silvery scale patch. Tergites II-VII with broad basolateral silvery patches, progressively more removed from base and extending more tergally on distal segments, on VIII usually merging with its mate middorsally; basomedian tergal light scaling present or absent on II-VII. Light scaling of sternites varied.

FEMALE GENITALIA (fig.16). Deeply retracted into segment VIII, even cerci usually invisible. Segment VIII partially retracted into segment VII, apex visible, numerous scales and bristles present; tergite about 0.6 length of tergite VII; sternite about 1.4 of tergite length and about 0.8 of sternite VII. Tergite IX strongly developed, about 0.5 of tergite VIII, undivided, without bristles. Sigma joined to cowl, narrow; continuous with poorly sclerotized insula which bears 2 pairs of setae. Cowl narrow, joined to base of postgenital plate; atrial plates absent. Postgenital plate shorter than cercus, bilobed. Tergite X not developed. Cercus broad, subequal in length to tergite IX or a little longer. Spermathecae 3, 1 a little larger than others.

MALES (fig.16). Coloration usually similar to females, sometimes light scales of torus absent (*allotecnion*) and rarely proboscis with a ventral light patch (*whitmorei*); sexual dimorphism of head appendages marked. Proboscis usually longer than in females. Palpus porrect, slender, subequal to proboscis; 5-segmented, segments 4 and 5 subequal, narrowed; entirely or predominantly dark scaled, light scales restricted to lower surface of segments 4 and 5; a few short inconspicuous setae on body of segment 4 and apex of segments 3 and 5. Whorls of flagellar segments 1-12 very strongly developed, usually with about 40 or more long bristles; flagellar segment 12 and 13 elongate, 12 about 1.25 of 13; torus greatly swollen. Claws of foreleg and midleg enlarged, unequal; larger claw with a blunt submedian tooth; both claws with or without an acute basal external tooth and with external basal spicules more numerous than in females, extending on shaft. Hindclaws as in the females.

MALE GENITALIA. Segment VIII long and wide, unspecialized. Segment IX moderately to strongly developed; tergite lobes indistinct or prominent and bearing a few to many moderate to strong setae, connected middorsally by a narrow sclerotized bridge, sternite strongly developed, usually with distinct median sclerotization bearing several pairs of setae distally. Sidepiece well developed; more or less conical or subcylindrical; mesal membrane developed from base to apex; tergomesal and/or sternomesal margins rarely (*Whitmorei* Group) with slight median lobes; with numerous long bristles and scales laterally and ventrally, tergal surface varied. Claspette rarely completely absent (*Whitmorei* Group), usually very poorly developed as a small sternal basomesal lobe bearing 1 or rarely 2 thickened apical setae and sometimes a few other less differentiated setae. Clasper simple, slender; 1 apical spiniform always present. Aedeagus without teeth; varied in shape, usually large; lateral sclerotization sometimes produced as a distal horn or lobe. Proctiger strongly developed, prominent; paraproct with a simple, large, heavily sclerotized, curved apical tooth; cercal setae distinct, short.

PUPAE. *Cephalothorax*: Middorsal ridge moderate; all hairs present, variously developed; hair 6-C always smaller than and cephalad of 7-C; hairs 8,9-C always widely separated and far caudad of trumpet base. *Trumpet*: Not placed on tubercle; varied in length; index from about 3.0 to 9.0; always without tracheoid; pinna short to long. *Metanotum*: Hairs 10,11-C removed from 12-C, moderately close together. *Abdomen*: Hairs 8,10,11-II apparently usually absent; hair 5-II,III usually caudad of hair 4; hair 1 usually most mesal hair on all segments; hair 9-VIII ventral in position, near

caudolateral angle or removed considerable distance cephalad; hairs 1-IX,X apparently not developed. Tergite IX strongly developed, its posterior margin smoothly rounded; cercal lobe of female projecting only a short distance beyond genital lobe. *Paddle*: Various developed; midrib usually strongly differentiated; marginal spicules varied.

LARVAE. *Head*: Width of head capsule subequal to length or slightly greater; labrum indistinctly differentiated, very narrow; mouthbrushes very numerous, filamentous; collar well developed, narrow; ventral part of head capsule (labial plate) rather short; posterior tentorial pit near caudal border; maxillary suture complete, sometimes extending caudolaterad of pit; cephalic border of labial plate truncate; aulacum with filamentous spicules; mental plate well developed. Hair 0-C distinct, far removed laterad of 1-C; 2-C apparently always absent; 3-C moderately developed; 11, 12, 14-C sometimes stellate. *Antenna*: Short to moderate in length; shaft with or without short spicules. Hair 1-A single to 3-branched. *Thorax*: Integument glabrous or with more or less distinct spicules. Hairs 0, 1, 3, 4, 8, 13, 14-P, 1, 13, 14-M, 1, 3, 4, 5, 8, 13-T sometimes stellate. Hairs 1-3-P on common tubercle, placed close to middorsal line; tubercles of 5-7-P usually distinctly joined (except in *Fulvithorax* Section); 9-12-P far ventrad, poorly developed, none of the hairs distinctly stellate. Hair 5-T always cephalad of hair 3. *Abdomen*: Integument as on thorax. Hair 12-I never developed, 9-I always ventrad of 7-I; hairs 1, 2, 5, 7, 9, 13 frequently stellate on segments I-VI; hair 6-I-VI always well developed, long; hair 7-I long. *Segment VIII*: Comb scales in a single regular row to an irregular patch of 3-5 rows. *Siphon*: Index varied from 2.0-9.0. Integument smooth, imbricate or spiculate. Pecten in a straight line, usually at least reaching to middle of siphon. Hair 1-S usually near middle; accessory hairs not developed. Acus varied or rarely absent (*walkeri*). *Anal Segment*: Saddle always incomplete; integument smooth, imbricate or spiculate; caudal margin with or without spines; acus absent. Ventral brush with 5 or 6 pairs of hairs, on a more or less distinctly sclerotized boss, with or without distinct grid bars.

DISCUSSION. For a general discussion of taxonomic characters, bionomics, distribution, systematics and affinities see the preceding chapter entitled "General Considerations."

The subgenus *Soperia* is here synonymized with *Howardina*. The taxon involved represents the Whitmorei Group of 2 species in the Sexlineatus Section, characterized primarily by the total absence of the claspette in the male genitalia. In other respects the Whitmorei Group obviously belongs in this section of *Howardina* and it is evident that there is a tendency within this subgenus to reduction in the claspette. Further, the name *Soperia* cannot be applied to the Whitmorei Group without recourse to the International Commission on Zoological Nomenclature since the nominal type species, *dominicii*, designated by Komp is a synonym of *sexlineatus* which obviously belongs to a different taxonomic group. In view of the above-mentioned taxonomic interpretation, there is no need at this time to request the Commission to vary the type species of *Soperia*, and this subgenus becomes a subjective synonym of *Howardina* by strict application of the rules in the current code.

KEYS TO SECTIONS

ADULTS

1. Prescutellar space with single median golden, yellow or silvery line; paratergite without scales **WALKERI SECTION**

- Prescutellar space with paired lateral white, yellow, golden or silvery lines;
paratergite with scales 2
- 2(1). Mesonotum with acrostichal line always dark . . **SEXLINEATUS SECTION**
Mesonotum with at least acrostichal line yellow or golden, sometimes anteri-
or half or more of mesonotum entirely or largely yellow or golden-scaled
. **FULVITHORAX SECTION**

MALE GENITALIA

1. Tergal surface of sidepiece with a very dense vestiture of large bristles ob-
scuring claspette area from dorsal aspect (*15. bahamensis*)
. in part **WALKERI SECTION**
Tergal surface of sidepiece with sparse vestiture of short or moderate bristles
not obscuring claspette area from dorsal aspect 2
- 2(1). Claspette completely absent (Whitmorei Group)
. in part **SEXLINEATUS SECTION**
Claspette represented by more or less strongly developed sternomesal lobe or
plaque bearing usually 1 thickened apical bristle, rarely 2 or more . . . 3
- 3(2). Sidepieces separated from each other at base sternally by a distance less than
maximum width of aedeagus **SEXLINEATUS SECTION**
Sidepieces separated from each other at base sternally by a distance greater
than maximum width of aedeagus 4
- 4(3). Claspettes connected across midline by more or less distinct sclerotized bar
. **FULVITHORAX SECTION**
Claspettes not connected across midline **WALKERI SECTION**

PUPAE

1. Hair 5-C longer than distance between its base and that of trumpet, always
double; hair 2-IV-VI usually within basal 0.66 of its tergite
. **SEXLINEATUS SECTION**
Hair 5-C shorter than distance between its base and that of trumpet, varied in
branching; hair 2-IV-VI usually distad of basal 0.75 of its tergite. . . . 2
- 2(1). Hair 9-VI minute, less than 0.5 of hair 2-VI. . . **FULVITHORAX SECTION**
Hair 9-VI subequal to or longer than hair 2-VI. . . . **WALKERI SECTION**

LARVAE

1. Caudal border of saddle without distinct marginal spicules; comb scales al-
ways in a patch of 3 or 4 irregular rows . . **FULVITHORAX SECTION**
Caudal border of saddle with conspicuous long marginal spicules; comb scales
usually in a single even row, rarely in a patch of 2-4 irregular rows (*16.*
busckii) 2
- 2(1). Hair 13-P not developed **WALKERI SECTION**
Hair 13-P present 3

- 3(2). Hair 9-P poorly developed, single (*Ioliota* Group)
 in part **WALKERI SECTION**
 Hair 9-P strongly developed, at least 4-branched . **SEXLINEATUS SECTION**

FULVITHORAX SECTION

FEMALES. Medium sized species, wing 2.8-3.6 mm. *Head*: Scales predominantly or entirely light, submedian and lateral dark patches sometimes large. Erect scales present on disc of vertex. Torus yellowish to dark brown, with a few moderately broad dark scales mesally. Palpus entirely dark scaled. *Thorax*: Mesonotum varying from nearly entirely golden or yellow to predominantly dark bronzy but with at least golden acrostichal line developed; median prescutellar light line not developed. Paratergite with scales. Acrostichal bristles absent on disc. Pleural scales silvery or dingy golden; *ppn*, *psp*, and *ssp* with scales; most of *mep* covered with large continuous scale patch. *Legs*: Midfemur and hindfemur without distinct distal light spot on anterior surface. Apex of tibia and base of tarsal segment 1 of all legs with white scales; all other tarsal segments dark. *Wing*: Veins entirely dark scaled. *Abdomen*: Sternites II-IV without dark scales.

MALES. Larger claw of foreleg and midleg with submedian tooth only.

MALE GENITALIA. Lobes of tergite IX indistinct to moderately prominent, with numerous strong setae. Sidepieces separated from each other at base by a distance greater than diameter of aedeagus at that level; tergomesal and sternomesal margins without any indication of lobes. Claspette prominent, connected at base with its mate by more or less distinct sclerotized bar; apical and subapical bristles varied in development.

PUPAE. *Cephalothorax*: Hair 5-C distinctly shorter than distance between its base and that of trumpet. *Abdomen*: Hair 5-IV,V usually single, extending beyond apex of tergite following; 2-IV-VI usually distad of 0.75 of its tergite; 9-II-VI cephalad of hair 6; 9-VII moderate to strong, close to hair 6, not removed cephalad.

LARVAE. Stellate hairs moderately developed. *Antenna*: Short; without spicules; hair 1-A single. *Thorax*: Integument glabrous; hairs 5-7-P on separate tubercles; hair 9-P usually single or double; hair 13-P absent. *Abdomen*: Integument glabrous; hairs 2,5,9-II-VII usually stellate, with few branches; hair 8-VII cephalodorsad of 9-VII. *Segment VIII*: Hair 5 stellate. Comb scales always in a patch of 3,4 irregular rows; individual scales rounded apically. *Siphon*: Index 2.2-2.3. Integument glabrous; pigmentation very strong. Acus distinct. Pecten teeth with basal denticles. *Anal Segment*: Saddle without marginal spicules. Hair 1-X short to moderate, double or triple; hair 3-X single, 2-X multiple. Ventral brush with 6 pairs of hairs arising from a strongly sclerotized boss.

DISCUSSION. The Fulvithorax Section is probably the most generalized lineage in *Howardina* and is strongly differentiated in all stages from all the other sections of the subgenus. The pattern of ornamentation of the mesonotum of the adults is unique in the subgenus and shows considerable variation whereas it is stabilized in the other sections. The male genitalia are readily recognized by the widely spaced sidepieces and the relatively large prominent claspette. The larvae are immediately separated from all the other sections by the characteristic comb patch and the absence of caudal marginal spicules on the anal saddle. The pupal stage has the simplest chaetotaxy in the limited branching and the relatively small size of the more conspicuous hairs. In nearly all these characters, the Fulvithorax Section shows the closest simi-

larity to the subgenus *Finlaya* from which *Howardina* was probably derived. Furthermore, as in typical American *Finlaya*, the natural breeding sites of the Fulvithorax Section are treeholes and broken bamboo.

The Fulvithorax Section presents a challenging taxonomic problem, which, unfortunately, I have not been able to resolve satisfactorily because of the absence of reared associated material from nearly all the critical areas of its wide reported distribution (fig.2) which is largely confined to the Atlantic drainages and extends from Nicaragua to southern Brazil. Formerly, 3 species with nearly overlapping distributions were recognized almost entirely on the basis of the extent and arrangement of the golden scaling of the mesonotum. The name *fulvithorax* was applied to forms with the mesonotum nearly entirely golden, *septemstriatus* to specimens with discrete lines of golden scales separated by dark scales, and *arborealis* to specimens intermediate in this respect. This situation suggested that only 1 very variable species was involved. However, closer analysis of the adults available for the present study and the examination of associated reared immature stages from 3 areas reveals a much more complex situation.

In the present study, I am recognizing only 1 group with 5 different forms in the Fulvithorax Section: *fulvithorax*, with a wide distribution from Venezuela and Trinidad to southern Brazil and occurring a considerable distance inland in Brazil and Peru; *septemstriatus*, restricted to lowland and moderate elevations in Nicaragua, Panama and Colombia; *arborealis*, from the Guianas and the lower Amazon; *aureolineatus*, primarily from the state of Bahia but apparently extending north to Para and south to Rio de Janeiro; and the unnamed Iquitos form from Peru which may be an inland type of *arborealis*. *A. fulvithorax*, *septemstriatus* and *arborealis* all show more or less distinct north-south clines in the extent of mesonotal golden scales, the southern populations being in general darker. In the case of *fulvithorax*, the inland populations also tend to be darker than the coastal. In any given area, only 2 of these forms appear to be present, except that 3 may occur in Para, and in all instances the different sympatric forms are quite distinct, without any intermediates. This suggests that distinct species are involved. However, the material available for this study is very limited and it is possible that the 5 forms recognized here are only subspecifically distinct and that there might be intergradations between them. It is even possible that only 1 very variable species is involved. The problem cannot be definitely resolved without progeny and individual rearings from areas of contact and overlap.

KEYS TO SPECIES

ADULTS

- 1. Mesonotum usually entirely golden-scaled from anterior promontory to wing root, rarely a few darker scales along dorsocentral lines posteriorly; no conspicuous dark bronzy scales on fossa 1. *fulvithorax*
- Mesonotum not entirely golden-scaled in anterior portion, with at least some conspicuous dark bronzy scales on fossa, usually with a more or less conspicuous linear pattern of golden scales surrounded by dark bronzy scales 2
- 2(1). Central part of anterior mesonotum with at least anterior inner dorsocentral lines golden in addition to the acrostichal line 3
- Central part of anterior mesonotum with only the acrostichal line golden 4

- 3(2). Lateral mesonotal light line conspicuous anteriorly, broad, not interrupted at or before scutal angle 2. *septemstriatus*
 Lateral mesonotal light line either completely absent or very narrow or interrupted at scutal angle 3. *arborealis*
- 4(2). Posterior outer dorsocentral golden line distinct, linear . . . 4. *aureolineatus*
 Posterior outer dorsocentral golden line represented by a patch caudad of scutal angle 5. *Iquitos form*

MALE GENITALIA

(5. *Iquitos form* unknown)

1. Subapical seta of claspette usually less than 0.7 of length of apical, latter not reaching middle of sternomesal margin of sidepiece
 1. *fulvithorax*; 2. *septemstriatus*
 Subapical seta of claspette usually subequal in length to apical, latter extending beyond level of middle of sternomesal margin of sidepiece. 2
- 2(1). Several subapical setae of claspette distinctly thickened . . . 4. *aureolineatus*
 None of the subapical setae of claspette thickened 3. *arborealis*

PUPAE

(4. *aureolineatus* and 5. *Iquitos form* unknown)

1. Hair 1-II usually with 4 or more branches. . . 1. *fulvithorax*; 2. *septemstriatus*
 Hair 1-II usually double 3. *arborealis*

LARVAE

(4. *aureolineatus* and 5. *Iquitos form* unknown)

1. Hair 6-C usually double; 11-C double; most pecten teeth without basal denticles 3. *arborealis*
 Hair 6-C single; 11-C with more than 2 branches; all pecten teeth with basal denticles 2
- 2(1). Hair 0-P long, usually 14-branched (10-21); gills moderate, broad, unequal .
 1. *fulvithorax*
 Hair 0-P short, usually 5-branched (4-6); gills long, slender and subequal. .
 2. *septemstriatus*

1. *Aedes* (Howardina) *fulvithorax* (Lutz)

Figs. 2, 8, 10, 11

1904. *Haemagogus fulvithorax* Lutz, 1904:47, 66, 73. TYPE: Holotype ♀, bridge Ipe-Arcado (Goias), Brazil, date and collector not specified [LU].
1906. *Taeniorhynchus palliatus* Coquillett, 1901a:61. TYPE: Holotype ♀, Trinidad, locality and date not specified, F.W. Urich [USNM, 9140]. Synonymy with *fulvithorax* by Howard, Dyar and Knab (1917:844).
1947. *Aedes* (Howardina) *tachirensis* Anduze, 1947:355-357. TYPE: Holotype ♀, Las Mesas de

Seboruco, Dto. Jauregui (Tachira), Venezuela, date and collector not specified [A]. Synonymy with *fulvithorax* by Lane (1951:335).

Aedes (Howardina) fulvithorax of Bonne and Bonne-Wepster (1925:373-375); Dyar (1928:228-229); Shannon (1931a:8,23,24,25; 1931b:142,143,146,161); Edwards (1932:155); Soper, Penna et al (1933:576); Lane (1936b:186); Whitman and Antunes (1937:819-821); Lane (1939:99); Floch and Abonnenc (1942a:5; 1942b:6); Anduze (1947:355); Lane (1951:335; 1953:706-708); Horsfall (1955:413,471,483); Martinez and Prosen (1955:29-31); Vargas (1956:22); Stone, Knight and Starcke (1959:174); Fauran (1961:29); Prosen, Carcavallo and Martinez (1964:104); Forattini (1965:400); Cova Garcia, Sutil and Rausseo (1966a:57,285; 1966b:11,73,141,169,333-334).

Aedes fulvithorax of Howard, Dyar and Knab (1912:65); Urich (1913:528); Howard, Dyar and Knab (1917:844-846); Dyar (1918:73,80); Costa Lima (1930:255); Davis and Shannon (1931:716,717,718); Martini (1931:206-208); Lane (1936a:131); Causey and Kumm (1948:475,476,477); Causey and Santos (1949:478); Causey, Kumm and Laemmert (1950:302,307); Matheson (1950:325); Delponte, Castro and Garcia (1951:239,240); Whitman (1951:263); Floch and Fauran (1954:48); Aitken (1960:4); Belem Virus Lab (1964:101,103); Bates (1949:205,320).

Gualteria fulvithorax of Theobald (1907:552); Peryassu (1908:45,179-180); Theobald (1910:607).

Haemagogus fulvithorax of Lutz (1905:67); Dyar and Knab (1906a:166,167).

Taeniorhynchus palliatus of Coquillett (1906b:24); Theobald (1910:432).

FEMALE. Wing: 2.97 mm. Proboscis: 2.34 mm. Forefemur: 2.16 mm. Abdomen: about 2.88 mm. *Head*: Scaling predominantly golden, a few dark scales present but not forming distinct lateral patches; narrow median scales occupying an extensive triangular area extending in the back to the outer erect scales and wide in front. Palpus about 0.19 of proboscis. Torus light brown to yellow, usually darkened on mesal surface. *Thorax*: Mesonotal integument yellowish to light brown; scaling usually entirely golden to just before level of prescutellar space; numerous linear dark bronzy scales along prescutellar rows, sometimes extending forward along dorsocentral bristles, a few similar dark scales in front of prescutellar space, a variable patch of similar dark scales above supraalar bristles, no dark scales on fossa; golden scales at scutal angle not markedly broadened (fig.8). Median scutellar lobe with numerous broad dark scales and a few golden in middle from base to apex; lateral lobes predominantly with narrow golden scales. Pleural scaling silvery, with slight yellowish tinge; *apn* predominantly with narrow scales, a few moderately broadened ones on lower and posterior parts; *ppn* with sparse vestiture of short linear golden scales, usually with only a few broadened scales in lower part. *Abdomen*: Median basal light patches usually present on tergites III,IV, light brown or golden; always present on V,VI, usually with slight yellowish tinge.

MALE. Wing: 2.36 mm. Proboscis: 2.1 mm. Forefemur: 1.49 mm. Essentially similar to female but lighter in color, dark scales of prescutellar area and midlobe of scutellum less numerous; *apn* with large patch of broad scales on lower posterior surface. Palpus distinctly shorter than proboscis.

MALE GENITALIA (fig.10). As figured; diagnostic characters as in the key. Ninth tergite lobe not prominent, with about 5 bristles. Claspette with subapical seta not thickened, less than 0.7 of apical, latter not reaching middle of sternomesal margin of sidepiece. Clasper with 1,2 subapical hairs.

PUPA (fig.10). Abdomen: 3.24 mm. Trumpet: 0.38 mm; index 4.5. Paddle: 0.73 mm. Chaetotaxy as figured; hairs moderately to darkly pigmented. Apparently indistinguishable from *septemstriatus* except perhaps by the longer trumpet. Readily separated from *arborealis* by hair 9-VI being minute, less than 0.5 of hair 2-VI, and more numerous branches in hairs 1-II, 9-VII,VIII. *Cephalothorax*: Mesonotum moderately

pigmented between trumpets; lateral areas and metanotum slightly darker. Hair 1(1, 1-2), 2(1), 3(1), 4(2), 5(2, 1-3), 6(1), 7(2, 1-3), 8(1, 1-3), 9(1), 10(2, 2-4), 11(1), 12(2, 1-4). *Abdomen*: Tergite I deeply pigmented except for usual membranous areas; tergite II uniformly moderately pigmented; tergites and sternites III, IV with moderate pigmentation but anterior border darker; rest of segments lighter. Segment I: hair 1(10-14 primary branches, each with many secondary ones), 2(2, 1-4), 3(1), 4(4, 2-6), 5(3, 2-5), 6(1), 7(2, 1-3), 9(1), 10(1, present on majority of specimens but sometimes absent on one side). Segment II: hair 0(1), 1(7, 4-13), 2(1, 1-2), 3(1, 1-3), 4(4, 3-5), 5(1, 1-2), 6(1, 1-2), 7(1, 1-4), 9(1). Segment III: hair 0(1), 1(2, 1-4), 2(1), 3(1), 4(3, 1-4), 5(1, 1-2), 6(1), 7(3, 2-4), 8(2, 1-3), 9(1), 10(1, 1-2), 11(1), 14(1). Segment IV: hair 0(1), 1(1, 1-2), 2(1), 3(3, 1-4), 4(2, 1-3), 5(1), 6(1), 7(3, 2-3), 8(2, 2-3), 9(1), 10(1, 1-3), 11(1), 14(1). Segment V: hair 0(1), 1(1, 1-2), 2(1), 3(1, 1-2), 4(2, 1-4), 5(1), 6(1), 7(3, 2-4), 8(2, 1-3), 9(1), 10(1, 1-2), 11(1), 14(1). Segment VI: hair 0(1, 1-2), 1(1), 2(1), 3(1), 4(1, 1-2), 5(1), 6(1), 7(1, 1-2), 8(2, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1), 6(2, 1-4), 7(1), 8(2, 1-3), 9(4, 3-5), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(7, 5-8), 14(1). *Paddle*: Uniformly lightly pigmented, midrib darker; external margin slightly serrated; hair 1-P slender; male genital lobe extending to about 0.37 of paddle, female genital lobe to 0.29.

LARVA (fig.11). Head: 0.89 mm. Siphon: 0.7 mm. Anal Saddle: 0.27 mm. Both hairy and nonhairy forms known. Very similar to *septemstriatus* from which it can be separated apparently by the longer, more profusely branched hair 0-P and the broad, short unequal gills. *Head*: Pigmentation moderate except around mouthparts where it is deeper; integument smooth. Mental plate with a strong median tooth and 11(11,12) distinct teeth on either side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(13, 10-16), 5(1), 6(1; moderate), 7(3, 2-4), 8(1), 9(2, 1-2), 10(1), 11(12, 11-16; stellate), 12(3, 2-4), 13(1), 14(4, 3-8), 15(2, 2-4). *Antenna*: Length about 0.48 of head; pigmentation deeper than on head capsule; all hairs single; hair 1 at 0.5 from base. *Thorax*: Apices of long hairs attenuate; barbs present on long and stellate hairs. Prothorax: hair 0(14, 10-21), 1(4, 3-4), 2(1), 3(7, 4-8), 4(4, 4-9), 5(2, 2-4), 6(1), 7(3, 2-3), 8(11, 8-18), 9(2, 1-5), 10(1), 11(3, 1-4), 12(1), 14(21, 17-28). Mesothorax: hair 1(5, 3-8), 2(1), 3(1), 4(1), 5(1), 6(5, 4-6), 7(1), 8(5, 4-7), 9(5, 4-7), 10(1), 11(2, 1-3), 12(1), 13(15, 12-23), 14(9, 8-16). Metathorax: hair 1(5, 4-12), 2(1), 3(4, 3-6), 4(6, 5-13), 5(5, 4-13), 6(1), 7(5, 4-8), 8(9, 8-22), 9(4, 3-5), 10(1), 11(1, 1-2), 12(1), 13(11, 8-18). *Abdomen*: Stellate hairs with branches of unequal length. Segment I: hair 1(8, 7-13), 2(10, 4-10), 3(1), 4(6, 5-6), 5(12, 10-13), 6(4, 3-4), 7(1, 1-2), 9(6, 5-8), 10(1), 11(12, 6-13), 13(8, 5-12). Segment II: hair 0(1), 1(10, 3-11), 2(9, 6-10), 3(1), 4(5, 3-8), 5(10, 7-11), 6(3, 3-4), 7(3, 2-7), 8(1), 9(8, 5-10), 10(1), 11(1), 12(1), 13(8, 5-14). Segment III: hair 0(1), 1(4, 2-8), 2(7, 7-9), 3(1), 4(1), 5(9, 6-12), 6(2), 7(6, 5-10), 8(1), 9(9, 6-13), 10(1), 11(1), 12(1), 13(6, 4-12), 14(1). Segment IV: hair 0(1), 1(5, 2-9), 2(8, 7-9), 3(1), 4(1), 5(9, 6-11), 6(2), 7(5, 5-8), 8(1), 9(8, 7-11), 10(1), 11(1), 12(1), 13(4, 2-10), 14(1). Segment V: hair 0(1), 1(3, 2-9), 2(7, 6-9), 3(2, 1-2), 4(1), 5(6, 6-9), 6(2), 7(5, 5-8), 8(1), 9(8, 6-10), 10(1), 11(1), 12(1), 13(5, 2-11), 14(1). Segment VI: hair 0(1), 1(5, 2-10), 2(7, 6-9), 3(1), 4(1), 5(7, 4-11), 6(1, 1-2), 7(4, 3-7), 8(1, 1-2), 9(4, 4-11), 10(1), 11(1), 12(1), 13(6, 5-13), 14(1). Segment VII: hair 0(1), 1(3, 2-8), 2(7, 6-10), 3(1), 4(1), 5(4, 3-8), 6(3, 2-3), 7(1), 8(5, 4-7), 9(4, 3-6), 10(1), 11(1), 12(1), 13(4, 3-10), 14(1). *Segment VIII*: Comb scales 20(19-24), in a patch of 3 irregular rows; individual scale elongate, rounded apically and evenly fringed with short spinules; hair 0(1), 1(5, 4-10), 2(1), 3(7, 5-8), 4(1), 5(6, 5-11), 14(1). *Siphon*: Index about 2.25-2.3; darkly pigmented

and with imbricate sculpturing throughout. Pecten extending to about 0.34-0.38; with 13 teeth (10-15), usually all with 1-3 basal denticles, terminal tooth not markedly enlarged. Hair 1(3, 3-4), 2(1), 3-5 not visible, 6(1), 7(1), 8(2, 1-3), 9(1). *Anal Segment*: Saddle darkly pigmented, with uniform imbricate sculpturing. Gills broad and short, unequal, ventral about 0.5 of dorsal. Hair 1(3, 2-7), 2(4, 3-5), 3(1), 4a(4, 3-5), 4b(3, 3-4), 4c(3), 4d(3, 3-4), 4e(3, 3-4), 4f(3, 2-4).

SYSTEMATICS. Adults of *fulvithorax* show considerable variation in thoracic ornamentation in different areas of the reported wide distribution of this species but are readily separated from the other species of the group by the much greater amount of golden scaling on the mesonotum in both males and females. The above descriptions of all stages are based entirely on material from Trinidad, the type locality of *palliatu*s. The single specimen I have seen from Venezuela, a female paratype of *tachirensis*, is indistinguishable from the Trinidad material. In these 2 northern populations, the integument of the thorax is light yellowish tan and the mesonotal scaling is bright yellow golden without any indication of dark scales on the fossa or anterior dorsocentral lines. The Surinam specimen agrees with this description also. The French Guiana material is similar in scaling but the thoracic integument is brown. As one proceeds south along the Atlantic lowlands of Brazil (Para, Bahia and Rio de Janeiro) the mesonotal golden scaling becomes darker, more coppery and the integument tends to become darker brown; however, in all these populations the fossa is without dark bronzy scales. At higher elevations in Brazil (Sao Paulo, Goias, Matto Grosso), the darkening of the integument and scaling becomes even stronger and there is a tendency for the appearance of a few dark bronzy scales in the fossa and along the posterior dorsocentral line. The single female from Iquitos resembles the interior populations of Brazil but has more extensive dark-scaled patches on the head than any other one I have seen.

In the scanty material of immature stages available from populations other than *palliatu*s, no striking differences are apparent.

No clear-cut separation can be made of *fulvithorax* from *septemstriatus* at this time in the pupal stage but the larvae of the 2 species are apparently distinct on the characters given in the key and diagnoses.

BIONOMICS. The immature stages of *fulvithorax* have been found only in tree-holes. The adults are primarily diurnal in activity but a few specimens have been collected at night.

Females feed readily on experimental animals in the laboratory. They have been investigated as possible vectors of yellow fever virus (Davis and Shannon 1931; Aitken 1960). The virus will survive and apparently develop in these mosquitoes as shown by successful infection of rhesus monkeys by inoculation of experimentally infected *fulvithorax* but all attempts to transmit the virus by bite have been negative.

DISTRIBUTION (fig.2). Lowlands to moderate elevations in Venezuela (Maracaibo and Orinoco drainages), Trinidad, Guyana, Surinam, French Guiana, Brazil (Amazon, Paraguay and Parana drainages, and states of Espirito Santo and Rio de Janeiro) and Peru (Amazon drainage). Material examined: 152 specimens; 20 ♂, 62 ♀, 29 pupae, 41 larvae; 30 individual rearings (4 pupal, 20 larval, 6 incomplete).

BRAZIL. *Bahia*: Piraja, 2 Apr 1929, [C. Davis and] R.C. Shannon, 2 lp, 2 ♂, 1 ♂ genitalia, 5 L, 6 l; 1938, 1 ♂; 1 l [USNM]. *Espirito Santo*: Santa Teresa, Apr 1940, 2 ♀ (Martinez and Prosen, 1955:31; MEPR). Valle do Chanaan, 173 ♀ (Davis and Shannon 1931:715; Whitman and Antunes 1937:819-820). *Goias*: Anapolis, Sept 1936, 1 ♂, 1 ♀ [USNM]. *Matto Grosso*: Guiaba, Feb 1935, 2 ♀; Mar 1935, 3 ♀ [USNM]. Maracaju, July 1937, 1 ♀; Nov 1937, 1 ♀; Dec 1937, 8 ♀; 3 ♀ [USNM]. Pocinho (Lane 1936b:186). *Minas Gerais*: Passos, 1945-47, 23A (Causey and Kumm

1948:475,477); 1840A (Causey, Kumm and Laemmert 1950:302,307); 386A (Causey and Santos 1949:478). *Para*: Belem, IAN forest, 105 ♀; IAN and Utinga forests, 9 ♀; Utinga forest, 9 ♀ (Belem Lab Report 1964:101,103,109,114). Belterra, June 1938, 1 ♀ [USNM]. Ilha de Marajo, 126 ♀ (Kumm and Novis 1938:502). Urucurituba, 18 Mar, C.H. Townsend, 1 ♀ [USNM]. *Rio de Janeiro*: Apr 1938, 4 ♀ [USNM]. *Sao Paulo*: Guariroba; Nhandeara; Nipoan; Planalto; Villa Poloni (Lane 1936a:131). *State not specified*: 1 ♂, 1 ♀ [USNM].

FRENCH GUIANA. Baduel (Fauran 1961:29). Balourou, Crique Anguille, Galion (Floch and Abonnenc 1947:10). Placer Isnard, June 1940, E. Abonnenc, 1 ♀ [UCLA] (Floch and Abonnenc 1947:10; Fauran 1961:29). Rorota, 8 May 1941, E. Abonnenc, 1 ♂ [UCLA] (Floch and Abonnenc 1947:10). Souvenir (Floch and Abonnenc 1947:10). Locality not specified, 1944, 1 ♂, 1 ♀ [USNM].

GUYANA. Mazaruni, 25 June 1936, 1 ♀ [USNM]; 6 July 1936, Leslie, 1 ♂ (KO 208A-1) [UCLA].

PERU. Iquitos, Mar-Apr 1931, R.C. Shannon, 1 ♀ [USNM].

SURINAM. Moengo, 19 Mar 1946, H.H. Stage, 1 L [USNM]. Locality not specified, 1 ♀ (36-69) [ITH].

TRINIDAD. *Nariva*: Charuma forest, 27 Aug 1964, treehole, A. Guerra, 1 lp♀ (TR 634-108) [UCLA]. *St. Andrew*: Mt. Harris, elev. 250 ft, 16 July 1964, treehole, F. Powdhar (TR 566), 1 lp♂ (566-102), 1 lp♀ (566-108) [UCLA]. *St. George*: Arima, Aripo Valley, elev. 500 ft, 16 Apr 1964, bamboo, A. Guerra (TR 319), 1 lp♂ (319-148), 2 lp♀ (319-139,149), 1 p♀ (319-111), 2 lp (319-128,137), 1 L; Cumaca road, elev. 500 ft, 14 Jan 1965, A. Guerra, 1 ♀ (TR 943); Verdant Vale, elev. 1000 ft, 10 Sept 1964, treehole, A. Guerra, 2 lp♀ (TR 680-102,103) [UCLA]. Monos Island, Grand Fond, 17 May 1964, treehole, A. Guerra (TR 410), 2 lp♂ (410-106,107), 1 lp♀ (410-111); 1 Aug 1964, bamboo, R. Martinez (TR 584), 1 lp♀ (584-11), 1 p♂ (584-102); 2 Aug 1964, bamboo, R. Martinez (TR 591), 1 lp♂ (591-109), 4 lp♀ (591-113,114,119,121), 1 p♂ (591-108), 1 p♀ (591-107), 1 L [UCLA]; 17 Nov 1905, F.W. Urich, 3 ♂, 1 ♀; June 1906, 2 lp♀ (20-2,3), 1 l♀ (20-1), 1 lp (20-4), 4 ♀ [USNM]. San Rafael, Arena forest, Oct 1965, 2 ♀ (TR 1432), Dec 1965, 3 ♀ (TR 1441) [UCLA]. Port of Spain, 9 Sept, 1 ♀; 1 ♀ [USNM]. *County not specified*: 26 Aug 1945, 1 lp; 9 Sept 1945, 1 ♀ [USNM].

VENEZUELA. *Bolivar*: Distrito Heres (Anduze 1947:355). Rio Orocopiche (Cova Garcia, Sutil and Rausseo 1966b:73). *Tachira*: Chururu, Distrito Uribante (Anduze 1947:357). Las Mesas de Seboruco, Distrito Jauregui, June 1944, P.J. Anduze, 1 ♀ [USNM] (Anduze 1947:357; Cova Garcia, Sutil and Rausseo 1966b:73).

2. *Aedes* (Howardina) *septemstriatus* Dyar & Knab

Figs.2,8,12,13

1907. *Aedes septemstriatus* Dyar and Knab, 1907:10. TYPE: Holotype ♀ (8), Bluefields, Nicaragua, W.F. Thornton [USNM, 10144].

Aedes (Howardina) *septemstriatus* of Bonne and Bonne-Wepster (1925:366-367); Dyar (1925:141, 148; 1928:232-233); Shannon (1931:142,147); Edwards (1932:155); Lane (1939:100); Floch and Abonnenc (1942a:6; 1942b:5; 1944:4; 1947:10); Martinez and Prosen (1955:27-29); Reyes (1955:74,89); Trapido, Galindo and Carpenter (1955:530,537,538); Trapido and Galindo (1957:122,125); Stone, Knight and Starcke (1959:174); Fauran (1961:29); Belkin, Schick and Heinemann (1965:42); Prosen (1965:42); Forattini (1965:239,242,403-404).

Aedes septemstriatus of Theobald (1910:485); Howard, Dyar and Knab (1917:846-847); Dyar (1918:73); Komp (1936:63); Antunes (1937a:16; 1937b:76); Arnett (1949:238); Galindo, Trapido and Carpenter (1950:102,104,105,108,112,113); Carpenter and Peyton (1952:681); Galindo, Carpenter and Trapido (1955:163); Reyes (1955:75); Komp (1956:39); Stone and Knight (1956:225); Blanton and Peyton (1958:31-32).

Aedes arborealis of Antunes (1937b:76); Reyes (1955:74,89); Boshell-Manrique and Osorno-Mesa (1944:177).

FEMALE. Wing: 3.15 mm. Proboscis: 2.53 mm. Forefemur: 2.01 mm. Abdomen: about 2.8 mm. *Head*: A large patch of broad dark scales on each side of a narrow median stripe of narrow golden scales, this stripe narrowed caudad. Palpus about 0.14 of proboscis. Torus dark brown. *Thorax* (fig.8): Mesonotal integument dark brown; mesonotum with a striking pattern of golden lines on a field of dark bronzy scales, latter sometimes with a few scattered golden scales; golden scaled lines as follows, narrow acrostichal bifurcating at prescutellar space, narrow inner dorsocentral not always reaching prescutellar space, outer dorsocentral arising at about level of scutal angle where it is broad and extending as a narrow line to scutellum; lateral marginal line broad, golden, interrupted in front of wing root, golden scales at scutal angle broader than in *fulvithorax*; fossa predominantly with dark bronzy scales, but sometimes with some scattered golden scales; space dorsad of supraalars with a large conspicuous patch of dark bronzy scales. Scutellar ornamentation as in *fulvithorax*. Pleural scaling denser and more silvery than in *fulvithorax*; scales of *apn* predominantly broad and very dense; *ppn* scale patch more extensive than in *fulvithorax* and with distinct broad scales in lower part. *Abdomen*: Median basal tergal light patches essentially as in *fulvithorax* except that scales on V, VI more silvery, without distinct yellow tinge.

MALE. Wing: 2.7 mm. Proboscis: 2.57 mm. Forefemur: 1.84 mm. Mesonotal ornamentation markedly different from female; anterior part predominantly with golden scales as in *fulvithorax* except for very narrow inconspicuous lines of dark bronzy scales on anterior dorsocentral lines and on each side of moderately broad acrostichal line, fossa usually without any bronzy scales; posterior part of mesonotum with more extensive pale scaling than in female but upper supraalar area with a distinct large patch of bronzy scales. Head with smaller dark patches than in female; palpus longer than in *fulvithorax*, subequal in length to proboscis.

MALE GENITALIA (fig.12). As figured; diagnostic characters as in the key. Extremely similar to *fulvithorax* but apparently with a more prominent IX tergite lobe with 8,9 bristles, and clasper with 2,3 longer subapical hairs.

PUPA (fig.12). Abdomen: 2.97 mm. Trumpet: 0.48 mm; index 4.3-4.5. Paddle: 0.76 mm. Only nonhairy form known. Extremely similar to and apparently indistinguishable from *fulvithorax*; separated from *arborealis* by the same characters as *fulvithorax*. Chaetotaxy as given below; hairs moderately to darkly pigmented. *Cephalothorax*: Mesonotum lightly pigmented; metanotum moderately pigmented; trumpet deeply pigmented and sharply contrasting. Hair 1(1), 2(1, 1-2), 3(1), 4(1, 1-2), 5(2, 1-3), 6(1), 7(2, 1-2), 8(1, 1-2), 9(1), 10(2, 1-3), 11(1), 12(2, 1-3). *Abdomen*: All abdominal segments lightly pigmented, first 3 segments slightly darker; anteromedian area of sternites III and IV with darker patches; integument imbricate. Segment I: hair 1(9-15 primary branches subequal in length and each with many secondary branches), 2(1), 3(1), 4(5, 2-6), 5(3, 2-5), 6(1), 7(1), 9(1), 10(1), and 11(1, found occasionally). Segment II: hair 0(1), 1(5, 2-7), 2(1), 3(1), 4(4, 2-6), 5(1, 1-2), 6(1), 7(1, 1-2), 8(1, found occasionally), 9(1). Segment III: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(2, 1-3), 5(1), 6(1), 7(3, 1-4), 8(2, 1-3), 9(1), 10(1, 1-2), 11(1), 14(1). Segment IV: hair 0(1), 1(1), 2(1), 3(2, 1-3), 4(1, 1-2), 5(1), 6(1), 7(2, 1-3), 8(2, 1-3), 9(1), 10(1, 1-2), 11(1), 14(1). Segment V: hair 0(1), 1(1), 2(1), 3(1, 1-2), 4(2, 1-3), 5(1), 6(1), 7(3, 1-4), 8(2, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1), 6(1), 7(1), 8(2, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1), 6(1, 1-2), 7(1), 8(2, 1-2), 9(3, 2-4), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(5, 4-6), 14(1). *Paddle*: Lightly pigmented, midrib slightly darker; apex not emarginated and with minute denticles; hair 1(1, 1-2). Male

genital lobe extending to 0.35 of paddle, female genital lobe to 0.31.

LARVA (fig.13). Head: 0.9 mm. Siphon: 0.78 mm. Anal Saddle: 0.32 mm. Only nonhairy form known. Very similar to *fulvithorax* but apparently distinct from the latter in the short hair O-P with few branches and gills long, slender and subequal. Chaetotaxy as given below; hairs moderately pigmented. *Head*: Pigmentation moderate except for areas around mouthparts where it is deeper. Mental plate with a strong median tooth and 12 distinct teeth (10-12) on each side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(15, 9-16), 5(1), 6(1), 7(4, 2-6), 8(1), 9(1), 10(1), 11(6, 3-7), 12(2, 1-3), 13(1), 14(2, 2-3), 15(2, 1-2). *Antenna*: Length about 0.41 of head; shaft uniform up to middle and then gradually narrowed distally; uniformly moderately pigmented, without spicules; all hairs single; hair 1 at about 0.5 from base. *Thorax*: Apices of long hairs attenuate; integument without spicules; stellate hairs with few branches. Prothorax: hair 0(5, 4-6), 1(3), 2(1), 3(3, 3-5), 4(3, 2-4), 5(3, 3-4), 6(1), 7(3, 2-3), 8(5, 5-8), 9(1, 1-2), 10(1), 11(2, 1-2), 12(1), 14(14, 10-18). Mesothorax: hair 1(3, 3-4), 2(1), 3(1), 4(1), 5(1), 6(5, 4-5), 7(1), 8(5, 5-6), 9(5, 5-7), 10(1), 11(1, 1-2), 12(1), 13(7, 3-8), 14(5, 3-5). Metathorax: hair 1(4, 3-5), 2(1), 3(3, 3-5), 4(3, 3-5), 5(5, 3-6), 6(1), 7(5, 5-7), 8(6, 4-7), 9(4, 3-5), 10(1), 11(1, 1-2), 12(1), 13(4, 3-6). *Abdomen*: Stellate hairs with fewer branches than in *fulvithorax*. Segment I: hair 1(5, 4-5), 2(6, 3-6), 3(1), 4(4, 2-8), 5(6, 5-7), 6(4, 3-4), 7(1), 9(3, 3-5), 10(1), 11(6, 5-8), 13(2, 2-5). Segment II: hair 0(1), 1(3, 2-4), 2(6, 5-8), 3(1), 4(3, 2-5), 5(5, 4-6), 6(3), 7(2, 1-3), 8(1), 9(4, 3-5), 10(1), 11(1), 12(1), 13(3, 2-5). Segment III: hair 0(1), 1(2, 1-4), 2(7, 4-7), 3(1), 4(1), 5(5, 3-5), 6(2), 7(4, 2-5), 8(1), 9(6, 4-7), 10(1), 11(1), 12(1), 13(2, 2-3), 14(1). Segment IV: hair 0(1), 1(2), 2(6, 5-8), 3(1), 4(1), 5(4, 4-6), 6(2), 7(3, 3-5), 8(1), 9(7, 4-7), 10(1), 11(1), 12(1), 13(2, 2-3), 14(1). Segment V: hair 0(1), 1(2, 1-2), 2(7, 5-8), 3(1), 4(2, 1-2), 5(5, 3-5), 6(2), 7(3, 3-4), 8(1), 9(6, 4-7), 10(1), 11(1), 12(1), 13(2, 1-3), 14(1). Segment VI: hair 0(1), 1(2), 2(6, 6-7), 3(1), 4(2, 1-2), 5(4, 3-5), 6(1, 1-2), 7(3, 3-5), 8(1), 9(4, 3-5), 10(1), 11(1), 12(1), 13(2, 2-4), 14(1). Segment VII: hair 0(1), 1(2), 2(6, 6-7), 3(1), 4(1), 5(3, 2-4), 6(2, 1-4), 7(1), 8(3, 2-5), 9(3, 3-4), 10(1), 11(1), 12(1), 13(2, 2-5), 14(1). *Segment VIII*: Comb scales usually 20(13-27), in 3 irregular rows, elongate, rounded apically and evenly fringed; hair 0(1), 1(3, 2-3), 2(1), 3(5, 4-6), 4(1), 5(4, 3-4), 14(1). *Siphon*: Index about 2.2-2.3; darkly pigmented and imbricate. Pecten extending to about 0.4; usually 15 teeth (12-15), smaller at base and gradually becoming larger distally, all with 1-3 basal denticles. Hair 1(3, 2-3), 2(1), 3-5 not visible, 6(1), 7(1), 8(2, 1-3), 9(1). *Anal Segment*: Saddle darkly pigmented and uniformly imbricate. Gills moderately long, narrow and subequal. Hair 1(2), 2(4, 3-5), 3(1), 4a(3, 3-4), 4b(2, 2-3), 4c(2, 2-3), 4d(2, 2-3), 4e(2, 2-3), 4f(2).

SYSTEMATICS. In the present interpretation, *septemstriatus* appears to be restricted to areas of rain forest, chiefly in the lowlands, in Nicaragua, Panama and Colombia. In the past it has been confused with *arborealis* and *aureolineatus* but it appears to be more closely related to *fulvithorax* on the basis of male genitalia and immature stages.

This species has a more marked sexual dimorphism in adult ornamentation than any other member of the group, the male approaching the condition in both sexes of *fulvithorax* and the female having a striking arrangement of golden and dark bronzy scales in lines on the mesonotum. In the area of overlap of the 2 forms in Colombia, *fulvithorax* and *septemstriatus* are very strongly differentiated and there is no indication of intergradation; for this reason *septemstriatus* is considered here to be a distinct species.

There is considerable variation in the ornamentation of the adults of *septemstria-*

tus but the available material is too scanty to determine whether this is entirely individual, ecological or geographical. However, it appears that in Colombia the light scaling is more restricted than in Panama and Nicaragua and particularly that the sexual dimorphism is not as marked. The above descriptions are based on individually associated material from Panama.

Although the adults of *septemstriatus* are usually readily separated from all other members of the group on the diagnostic characters in the key and descriptions, I have not been able to find any reliable characters to separate it in the pupal stage from *fulvithorax*. The larvae of the 2 species are also very similar and it is possible that some of the characters used to differentiate them are not reliable because only the nonhairy form of *septemstriatus* has been seen.

BIONOMICS. The immature stages of *septemstriatus* have been found in treeholes and broken bamboo. In one instance they were associated with 3 species of *Haemagogus*, *Aedes (F.) terreus*, 2 species of *Culex* and a species of *Sabethes* (Galindo, Carpenter and Trapido 1955). The adults are diurnal, primarily sylvan, and are found mainly at the forest floor and not in the canopy (Trapido, Galindo and Carpenter 1955; Trapido and Galindo 1957). Other published reports on the bionomics of *septemstriatus* (Kumm and Novis 1938; Causey and Santos 1949; Floch and Fauran 1954; Belem Virus Lab 1964) do not apply to this species and should probably be attributed to *arborealis*.

DISTRIBUTION (fig.2). Lowland to moderate elevations in Colombia (Upper Orinoco drainage), Costa Rica (Pacific side), Nicaragua (Atlantic side) and Panama (Atlantic and Pacific sides). Material examined: 151 specimens; 44 ♂, 57 ♀, 42 pupae, 8 larvae; 12 individual rearings (9 pupal, 3 larval).

COLOMBIA. *Meta*: Restrepo, 12 July 1935, W.H.W. Komp, 2 ♂ [USNM], 2 ♀ (KO 209A-9), 1 ♀ (KO 209A-11) [UCLA]; 22 July 1935, W.H.W. Komp, 9 ♂, 3 ♀, 2 ♀; July 1935, 1 ♂ genitalia, 1 L; 22 Aug 1935, W.H.W. Komp, 1 ♂ [USNM], 1 ♀ (KO 206A-1), 4 ♂, 8 ♀ (KO 206A-7), 1 ♂ (KO 206A-13) [UCLA]; 2 May 1942, W.H.W. Komp, 2 ♀; 1 ♀ [USNM]. Villavicencio, 16 July 1943, W.H.W. Komp, 1 ♀; 25 Oct 1943, M. Bates, 3 ♀; 1944, M. Bates, 1 p, 1 ♀ [USNM].

COSTA RICA. *Puntarenas*: Esquinas, elev. 300 ft, 6 June-30 Nov 1950, 1 A (Trapido, Galindo and Carpenter 1955:530).

NICARAGUA. Bluefields, W.F. Thornton, 2 ♀ topotypes [USNM].

PANAMA. *Bocas del Toro*: Almirante, Bocas-Chiriqui Road, 2 May 1963, A. Quinonez (PA 301), 3 1p♂ (301-106,109,112), 5 p♂ (301-102,105,108,110,111), 4 p♀ (301-101,103,104,109), 29 P. Chiriquisito, Trail Caldera, 5 Nov 1965, P. Orjuela (PA 1004), 5 ♀ [UCLA]. *Canal Zone*: Empire, 11 Feb 1926, J.B. Shropshire, 1 ♂. Fort Randolph, 27 July 1926, D.P. Curry, 1 ♂. France Field, 20 Feb 1926, J.B. Shropshire, 6 ♂, 19 ♀. Mojinga Swamp, 1 A (Blanton and Peyton 1958:32). Paja (=Nueva Emperador), 13 May 1941, G.B. Fairchild, 5 ♂, 1 ♀. Summit, 30 May 1938, W.H.W. Komp, 1 ♀; 7 May 1943, W.H.W. Komp, 1 ♂; 15 May 1945, W.H.W. Komp, 1 ♂; 1 ♀ [USNM]. *Chiriqui*: Chorchá, elev. 300 ft, 12 June-11 Dec 1950, 1 A (Trapido, Galindo and Carpenter 1955:530). David, C.S. Ludlow, 1 ♀ (Dyar 1923:148) [Army Medical Museum]. *Cocle*: Tucue, elev. 1000 ft, 12 June-14 Dec 1950, 14 A (Trapido, Galindo and Carpenter 1955:530). *Colon*: Candelaria, elev. 200 ft, 14-27 Aug 1950, 5 A (Trapido, Galindo and Carpenter 1955:530). *Panama*: Arraijan, elev. 600-800 ft, 5 June-29 Dec 1950, 2 A. Campana, elev. 2000 ft, 14 June-6 Dec 1950, 12 A. Campanita Arriba, elev. 600 ft, 24 Aug-4 Dec 1950, 14 A. La Victoria, elev. 400-1200 ft, 7 Feb-28 Dec 1950, 1 A (Trapido, Galindo and Carpenter 1955:530). Pacora area, 10 ♀ (Galindo, Trapido and Carpenter 1950:548,551). *San Jose Island*: 26 July 1944, W.H.W. Komp, 1 ♀ [USNM].

3. *Aedes (Howardina) arborealis* Bonne-Wepster & Bonne Figs.2,8,14,15

1920. *Aedes arborealis* Bonne-Wepster and Bonne, 1920:178. TYPE: Lectotype ♂ (3893) with associated larval and pupal skins (M 53) and genitalia slide (M 41), both slides marked BB 655, Dam, Surinam, Jan 1919, J. Bonne-Wepster and C. Bonne [ITH; selection of Belkin 1968].

Aedes (Howardina) arborealis of Bonne and Bonne-Wepster (1925:377-380); Dyar (1928:231-232); Edwards (1932:155); Lane (1936b:186; 1939:99); Floch and Abonnenc (1944:41; 1947:10); Lane (1953:708-710); Horsfall (1955:471); Stone, Knight and Starcke (1959:173); Floch and Fauran (1954:48); Fauran (1961:29); Belkin, Schick and Heinemann (1965:63); Forattini (1965:400); Stone (1967:208).

Aedes septemstriatus of Kumm and Novis (1938:502,507,510-511); Causey and Santos (1949:478); Floch and Fauran (1947:10; 1954:48); Fauran (1961:29); Belem Virus Lab (1964:101, 103,109,112).

FEMALE. Wing: 2.8 mm. Proboscis: 2.45 mm. Forefemur: 1.93 mm. Abdomen: about 2.63 mm. In most respects intermediate between *fulvithorax* and *septemstriatus* but differing from both in the following. *Head*: Median line of golden scales very narrow, these scales linear; submedian dark patches distinct but smaller than in *septemstriatus*. *Thorax* (fig.8): Mesonotum predominantly with golden yellow scales anteriorly; ornamentation superficially very similar to ♀ of *septemstriatus* except that golden acrostichal line narrower, fossa predominantly with bronzy scales, and marginal golden area interrupted in front as well as caudad of scutal angle; caudal part of mesonotum with dark scaling more extensive than golden; upper supraalar patch of dark scales conspicuous. Scutellum with a conspicuous median line of golden scales. Scales of *apn*, *ppn*, and *ppl* golden, remaining pleural scales silvery; *apn* with numerous dense broad scales; *ppn* patch restricted, without broad scales. *Abdomen*: Median basal tergal patches as in *septemstriatus* on VI,VII but apparently small and yellowish on IV,V.

MALE. Wing: 2.8 mm. Proboscis: 2.62 mm. Forefemur: 1.75 mm. Mesonotal ornamentation essentially as in the female but golden scales more numerous; acrostichal golden line broad; paraacrostichal dark-scaled line very narrow; outer dorsocentral dark line evident only posteriorly; fossa with small patch of dark bronzy scales; lower part of *ppn* with a few broad scales. *Head*: Without distinct dark patches, with only a few dark scales. Palpus subequal to proboscis in length, with numerous pale scales on lower basal surfaces of segments 3 to 5.

MALE GENITALIA (fig.14). As figured; diagnostic characters as in the key. In general similar to *fulvithorax* except for the following. Ninth tergite lobe indistinct, with 6,7 strong bristles. Claspette with subapical seta subequal to apical but not markedly thickened; other setae much longer than in *fulvithorax*, apical seta extending beyond middle of sternomesal margin of sidepiece. Clasper with about 5 setae in distal half.

PUPA (fig.14). Abdomen: 3.24 mm. Trumpet: 0.44 mm; index 3.3-3.4. Paddle: 0.65 mm. Only nonhairy form known. Readily differentiated from *fulvithorax* and *septemstriatus* by fewer branches in hairs 1-II, 9-VII,VIII and broader paddle. Chaetotaxy as given below; hairs moderately to darkly pigmented. *Cephalothorax*: Mesonotum between trumpets moderately pigmented, darker laterad; metanotum moderately pigmented; trumpets darkly pigmented and strongly contrasting. Hair 1(1), 2(1), 3(1), 4(1, 1-2), 5(1, 1-2), 6(1, 1-2), 7(1, 1-2), 8(2, 2-3), 9(1), 10(2), 11(1), 12(1). *Abdomen*: Tergite I moderately pigmented except for usual light membranous areas; other segments moderately pigmented and integument imbricate; pigmentation progressively lighter caudad. Segment I: hair 1(5-7 main branches, subequal in length and each with many secondary branches), 2(1), 3(1), 4(2, 2-4), 5(1), 6(1), 7(1, 1-2),

9(1). Segment II: hair 0(1), 1(2, 1-4), 2(1, 1-2), 3(1), 4(4, 1-4), 5(1), 6(1), 7(1, 1-2), 9(1). Segment III: hair 0(1), 1(1), 2(1), 3(1, 1-2), 4(1, 1-3), 5(1), 6(1), 7(2, 1-4), 8(2, 1-2), 9(1), 10(1, 1-2), 11(1, 1-2), 14(1). Segment IV: hair 0(1), 1(1), 2(1), 3(2, 2-3), 4(1, 1-3), 5(1), 6(1), 7(1, 1-2), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment V: hair 0(1), 1(1), 2(1), 3(1), 4(2, 1-3), 5(1), 6(1), 7(1, 1-2), 8(2, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1), 6(1), 7(1), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1), 6(1), 7(1), 8(1), 9(2, 1-2), 10(1), 11(1), 14(1). *Segment VIII*: hair 0(1), 4(1), 9(3), 14(1). *Paddle*: Ovoid; lightly pigmented, midrib dark; apex slightly produced; hair 1 single; male genital lobe extending to 0.6 of paddle, female genital lobe to 0.34.

LARVA (fig.15). Only nonhairy form known. Readily differentiated from *fulvithorax* and *septemstriatus* by the following. Head hairs 6,11-C usually double; stellate hairs with heavier spikes; comb scales usually more numerous (27-39), in 4,5 rows, siphon index about 2.0; 10-11 pecten teeth without basal denticles, the distal teeth greatly elongate; anal gills shorter than saddle, broad and subequal.

SYSTEMATICS. As indicated in the diagnosis above, *arborealis* is somewhat intermediate between *fulvithorax* and *septemstriatus* in the ornamentation of the adults. Its larva and pupa are quite distinct from these species but may be similar to the unknown immature stages of *aureolineatus* which appears to be closely related to *arborealis*.

In the present interpretation, *arborealis* has a more restricted distribution than formerly reported, being confined to the Guianas and the lower Amazon. Former reports of *arborealis* from Colombia pertain to *septemstriatus* and all the specimens from the lower Amazon identified as *septemstriatus* in USNM appear to be *arborealis*.

The above descriptions are based on the type series from Surinam. Specimens from Guyana and French Guiana agree in all respects with the Surinam material. The adults from the lower Amazon are usually considerably darker, with more extensive dark bronzy scaling on the mesonotum, but there is a great deal of variation in this character and some specimens are indistinguishable from the material from French Guiana. I consider all these populations as members of a single species.

A single specimen of *aureolineatus* from Para without specified locality, suggests that this species and *arborealis* may overlap in the lower Amazon but there is no indication of intergradation of the 2 forms in the material at hand from Belem and up-river.

BIONOMICS. The immature stages of *arborealis* have been found in treeholes only. There are no published reports on the adult bionomics of *arborealis* but the records of *septemstriatus* taken on human bait (Belem Virus Lab 1964) and during the wet (Oct-Mar) and dry seasons (Causey and Santos 1949) undoubtedly refer to *arborealis* in the present sense.

DISTRIBUTION (fig.2). Confined to low elevations in Guyana, Surinam, French Guiana and Brazil (lower Amazon drainage). Material examined: 80 specimens; 8 ♂, 57 ♀, 6 pupae, 9 larvae; 7 individual rearings (3 larval, 4 incomplete).

BRAZIL. *Para*: Belem, July 1931, R.C. Shannon, 1 ♀ [USNM]; IAN Forest, 413 ♀; IAN and Utinga forests, 18 ♀; Utinga Forest, 107 ♀ (Belem Lab Report 1964:101,103,109,112). Currallinho, 1 Apr 1936, 1 ♀; Apr 1936, 1 ♀; 26 July 1936, 1 ♂, 1 ♀; 1936, 1 L; 2 ♀ (K 325,341); Mar 1938, 5 ♀ [USNM]. Ilha de Marajo, 1 ♀ (Kumm and Novis 1938:507). Santarem, Belterra, Aug 1938, 1 ♀; Oct 1938, 1 ♀ [USNM].

FRENCH GUIANA. Baduel (Floch and Abonnenc 1944:4; 1947:10). Cayenne, Apr 1943, 1 ♀ [USNM]; June 1944, E. Abonnenc, 32 ♀. Cabassou, 4 Feb 1965, T.H.G. Aitken, R. Martinez and A. Guerra (FG 46), 1 ♂ [UCLA]. Iracoubo (Fauran 1961:29). Placer Isnard, 17 June 1940, E. Abonnenc, 2 ♀ [UCLA]. Rorota, 8 May 1941, 2 ♀, 3 lp (577,578) [USNM].

GUYANA. Mazaruni, 25 June 1936, W.H.W. Komp, 2 ♀ [USNM]; 6 July 1936, Leslie, 1 ♂, 2 ♀ (KO 208A-7); 6 July, 1 ♂ (KO 208A-8); 1 ♂ (KO 208A-10) [UCLA].

SURINAM. Aloesoebanja, 17 Jan 1956, E. van der Kuyp, 1 L. Dam, 1 lp♀, "cotype" [USNM, No.22712]; 1 lp♀ (39-09, "cotype"), 1 lp (39-01); 1 ♂ (38-98, "cotype") [UCLA].

4. *Aedes (Howardina) aureolineatus* Berlin, n.sp.

Figs.2,8,58

TYPES: Holotype ♀, Piraja (Bahia), Brazil, May 1931, Servico Febre Amarela, M.E.S., Brasil [USNM]. Allotype ♂ (660121-10) with genitalia slide, same data as holotype [USNM]. Paratypes: 2 ♀, same data as holotype [USNM, UCLA].

FEMALE. Wing: 3.6 mm. Proboscis: 2.7 mm. Forefemur: 2.32 mm. Abdomen: about 3.33 mm. *Head*: Median line of golden scales very narrow; these scales broader than in *fulvithorax* and curved; submedian dark patch very large, extending to occiput; a small elongate lateral dark line at level of middle of *apn*. Palpus about 0.19 of proboscis. Torus light yellowish brown, darkened on mesal surface. *Thorax* (fig.8): Mesonotal integument brown; scaling predominantly dark bronzy; a conspicuous acrostichal golden line from anterior promontory, bifurcating on prescutellar space and reaching scutellum; a golden outer dorsocentral line arising caudad of scutal angle, broad and curved outward anteriorly, narrow posteriorly and reaching scutellum; lateral margin golden scaled, broadly to level of middle of *ppn*, narrowly to scutal angle, broadly caudad of scutal angle, separated by dark scales from a very large golden patch in and above supraalars; a few scattered golden scales laterad of acrostichal line especially in front. Scutellum with a conspicuous median line of narrow golden scales. Paratergite as in *fulvithorax*. Scales of *apn* numerous, light golden, moderately broad and curved; *ppn* patch extensive, light golden, scales short and curved; remaining pleural scale patches silvery to very light golden. *Abdomen*: Median basal tergal light patches silvery on VI,VII, light brown on V, usually absent on other segments.

MALE. Wing: 3.06 mm. Proboscis: 3.1 mm. Forefemur: 2.16 mm. Allotype lacking proboscis, 1 antenna, palpi and all legs on right side; description from Salvador specimen. Essentially similar to female except that scattered golden scales more numerous and lateral marginal light line wider on mesonotum. Palpus subequal to proboscis in length.

MALE GENITALIA (fig.58). As figured; diagnostic characters as in the key. Essentially as in *arborealis* except that lobe of tergite IX more prominent and several setae of the claspette distinctly thickened.

IMMATURE STAGES. Unknown.

SYSTEMATICS. The adults of *aureolineatus* are strikingly different from all other members of the group except *sp. 5 (Iquitos form)* in the reduction of the golden scaling on the central anterior part of the mesonotum to a narrow acrostichal line. This form appears to be a distinct species probably related to *arborealis*, but this cannot be definitely determined until the immature stages are found.

In the small series of *aureolineatus* very little individual variation is evident. The specimens from Para and Rio de Janeiro are not significantly different from the type material from Bahia.

BIONOMICS. Nothing is known of the breeding sites and adult bionomics of *aureolineatus* but it is likely that they are similar to other members of this group.

DISTRIBUTION (fig.2). Confined to low elevations in Brazil along the coast from Para to Rio de Janeiro.

BRAZIL. *Bahia*: Piraja, May 1933, 1 ♂, 3 ♀, type series [USNM, UCLA]. Salvador, 27 Apr 1936, E. Silva, 1 ♂ [USNM]. *Para*: Apr 1930, N.C. Davis, 1 ♀ [USNM]. *Rio de Janeiro*: Apr 1933, 1 ♀ [USNM].

5. *Aedes* (Howardina) sp., Iquitos form

FEMALE. Wing: 3.33 mm. Proboscis: 2.71 mm. Forefemur: 2.34 mm. Abdomen: broken off. Extremely similar to *aureolineatus* and differing apparently chiefly in the following. Mesonotal ornamentation darker; acrostichal golden line narrower; dorso-central golden line represented only by a rounded spot at about 0.5 of mesonotum; fewer scattered golden scales; *apn* scales more numerous and broader, more distinctly silvery; *ppn* scale patch more extensive, with some broad scales below.

MALE and IMMATURE STAGES. Unknown.

DISCUSSION. The single specimen from Iquitos, Peru, Mar-Apr 1931, R.C. Shannon [USNM] lacks the abdomen. It may represent a distinct species related to *arbor-ealis* and *aureolineatus* or a local population of one of these. This form shows the greatest reduction in the golden scaling on the anterior part of the mesonotum in the Fulvithorax Group.

WALKERI SECTION

FEMALES. Usually small to medium sized species, wing 2.1-3.5 mm. *Head*: Submedian dark patch broad; lateral patch smaller, bordered posteriorly by light scales. Erect scales varied. Torus brown to dark brown, with a few small black scales mesally. Palpus with or without apical light scales. *Thorax*: Mesonotum usually with distinct linear light pattern (except in some *grabhami*), light scales all golden or combination of golden and silvery. Acrostichal line absent but a small light patch present at level of anterior promontory; inner and outer dorsocentral lines incomplete, inner not reaching scutellum, outer usually not reaching anterior margin; lateral marginal line broken at scutal angle, usually narrow (very broad in Walkeri Group); median prescutellar line present. Paratergite bare. Acrostichal bristles usually absent on disc, present in Busckii Group. Pleural scales silvery (fig. 17); *ppn* and *psp* without scales; *ssp* scale patch present or absent; *mep* with a small, restricted patch at upper half below bristles only. *Legs*: Midfemur and hindfemur without distinct distal light spot on anterior surface. Foretibia sometimes with light scales distally. Tarsal light markings not restricted to segment 1. *Wing*: Veins entirely dark scaled. *Abdomen*: Sternites II-IV without dark scales.

MALES. Larger claws of foreleg and midleg with both submedian and basal teeth present (in Busckii Group basal tooth absent).

MALE GENITALIA. Lobes of tergite IX indistinct, bearing a few strong setae. Sidepieces separated from each other at base by a distance greater than diameter of aedeagus at that level; tergomesal and sternomesal margins without any indication of lobes. Claspette represented by a small roughly triangular or fingerlike lobe bearing 1, rarely 2, apical setae; not connected to its mate.

PUPAE. *Cephalothorax*: Hair 5-C usually shorter than distance between its base and that of trumpet; either subequal to or longer than hair 4-C; if longer, varied in branching. *Abdomen*: Hair 5-IV,V usually single (double or triple in Aurites and Busckii Groups), terminating before or extending beyond apex of tergite following;

2-IV-VI usually distad of 0.75 of its tergite; 9-III-VI usually caudolaterad of hair 6 (except in *walkeri*); 9-VII moderately to strongly developed, either close to or removed considerable distance cephalad of hair 6.

LARVAE. Stellate hairs developed or not. *Antenna*: Short; with or without scattered spicules; hair 1-A single. *Thorax*: Integument glabrous. Tubercles of hairs 5-7-P distinctly joined; hair 9-P simple, usually single or double; hair 13-P absent except in Ioliota Group. *Abdomen*: Integument glabrous except in *walkeri* and members of Ioliota Group. Hairs 2,5,9-VII usually stellate; hair 8-VII cephalad or cephalodorsad of 9-VII. *Segment VIII*: Hairs 1,5-VIII usually strong, with a few branches but not stellate. Comb scales usually in a single row (up to 2-4 irregular rows in Busckii Group); individual scale usually blunt apically. *Siphon*: Index 2.0-8.5. Integument smooth, imbricate or spiculate. Acus distinct except in Walkeri and Aurites Groups. Pecten teeth with or without basal denticles. *Anal Segment*: Saddle with distinct marginal spicules. Hair 1-X short to moderate, with a few branches; hair 3-X single, 2-X multiple. Ventral brush with 5 or 6 pairs of hairs arising from a boss with or without distinct grid bars.

DISCUSSION. The Walkeri Section is the most heterogeneous of the 3 sections in the subgenus, particularly in the immature stages. However, it is probably a monophyletic lineage characterized by 3 unique features of adult ornamentation: paratergite and *ppn* both without scales and prescutellar area with a median light-scaled line.

Four rather distinct phylads within the section are suggested by differences in the mesonotal pattern of the adults: (1) Aurites Group, with a rather broad linear golden pattern very reminiscent of the Sexlineatus Section, (2) Walkeri Group, with a very broad continuous lateral silvery patch and apparently relatively broad golden dorso-central lines, (3) the very similar Ioliota and Albonotatus Groups, with a very narrow silvery lateral line, very faint golden dorsocentral lines and a silvery prescutellar line, and (4) Busckii Group, intermediate between the Walkeri Group and the Ioliota-Albonotatus Groups in the width of the lateral silvery line which is frequently broken. The Busckii Group is unique in the subgenus in the presence of acrostichal bristles on the disc of the mesonotum.

The immature stages are much more diverse than in the other sections, each of the above-mentioned phylads possessing a type quite as distinct as those characterizing the Sexlineatus and Fulvithorax Sections. The Ioliota Group is also clearly separated in the larval and pupal stages from the Albonotatus Group. The breeding sites in the Walkeri Section encompass the entire range used by the subgenus, extending to habitats not utilized by the other sections.

The Walkeri Section is almost entirely confined to islands in the Caribbean area. Only 2 small encroachments on present continental areas are known: (1) in the Yucatan Peninsula by the Ioliota Group and (2) in northern Venezuela and Trinidad by the Ioliota Group and northern Venezuela only by the Walkeri Group. The groups show primarily allopatric complementary distributions. The only exceptions known are in (1) the Walkeri and Aurites Groups in Jamaica, (2) possibly Albonotatus and Busckii Groups in Guadeloupe, and (3) Ioliota and Walkeri Groups in northern Venezuela. Except in the Aurites Group, members of a group always have allopatric distributions (fig.3).

There are 2 surprising gaps in the distribution of the Walkeri Section. Although intensive collections have been made in Puerto Rico, Virgin Islands and Leeward Islands, no species of *Howardina* has yet been recorded from this area. Nor has the subgenus been recorded from Cuba. However, it is possible that the record of *Haemagogus* sp. from Cuba by Montchadsky and Garcia (1966:46-47) is based on a mis-

identification of an undescribed species of *Howardina*.

The diversity of types in the Walkeri Section is undoubtedly a reflection of typical insular speciation through isolation of small populations. As indicated above, it appears that only one original stock was probably involved, although there is a suggestion of a possible recent intrusion of the Sexlineatus Section in the Aurites Group (see). However, the present pattern could not have been attained through a simple splitting of the original stock among the island masses as they exist today. The retention of such primitive features as acrostichal bristles in the adults of *busckii*, hair 13-P in the larvae of the Ioliota Group, 6 pairs of hairs in the ventral brush in all species except *busckii* and a patch of comb scales in the larvae of some populations of *busckii*, is indicative of very early separation of the Walkeri Section from the other sections rather than its recent derivation from one of them. That the present pattern represents speciation and dispersal on island masses no longer in existence in the Caribbean area is strongly supported by the relict distributions of the Walkeri and Ioliota Groups.

KEYS TO GROUPS AND SPECIES

ADULTS

- 1. All mesonotal light scaling golden (Aurites Group) 2
- At least lateral marginal line silvery or white 4

Aurites Group

- 2(1). Pleuron with a large silvery patch continuous from lower *pra* across posterior *stp* to its lower margin 8. *aurites*
- Pleuron with 3 small discrete, separate silvery patches, one each on lower *pra*, upper *stp* and lower *stp* 3

- 3(2). Antealar area (above paratergite) with golden scales, rarely 1-3 bronzy scales present; mesonotal light lines usually distinct and broad, sometimes almost completely merging in anterior two-thirds of mesonotum . . 9. *grabhami*
- Antealar area with numerous dark bronzy scales above narrow posterior lateral mesonotal golden line; mesonotal light lines narrow, discrete, never merging 10. *inaequalis*; 11. *stenei*

- 4(1). Lateral marginal line broadened to form a conspicuous lateral silvery patch; *ssp* without scales (Walkeri Group) 5
- Lateral marginal line very narrow, not extending on fossa; *ssp* with patch of silvery scales. 6

Walkeri Group

- 5(4). Inner dorsocentral line continuous, moderately broad 6. *walkeri*
- Inner dorsocentral line dotted, only faintly indicated 7. *argyrites*

Busckii Group

- 6(4). Median prescutellar line golden, faint; palpus entirely dark in both sexes; acrostichal bristles present on disc 12. *busckii*

Median prescutellar line silvery, conspicuous; silvery scales on apex of female palpus and base of some segments of male palpus; acrostichal bristles absent on disc 7

- 7(6). Hindtarsal segment 5 with white scales (Ioliota Group) 8
Hindtarsal segment 5 with black scales only (Albonotatus Group) 9

Ioliota Group

- 8(7). Hindtarsal segment 5 entirely white-scaled 12. *ioliota*
Hindtarsal segment 5 with some apical and posterior dark scales
. 13. *cozumelensis*

Albonotatus Group

- 9(7). Hindtarsal segment 3 white-scaled in barely more than basal 0.5
. 15. *bahamensis*
Hindtarsal segment 3 white-scaled in at least basal 0.7 14. *albonotatus*

MALE GENITALIA

(7. *argyrites* not definitely known)

1. Tergal surface of sidepiece with very dense vestiture of long bristles, some as long as sidepiece 15. *bahamensis*
Tergal surface of sidepiece with sparse vestiture of short or moderate bristles, none more than 0.5 of sidepiece length 2
- 2(1). Clasper very long, including spiniform about as long as sidepiece
. 14. *albonotatus*
Clasper short or moderate, including spiniform not more than 0.75 of sidepiece length 3
- 3(2). Claspette with an apical fingerlike cylindrical process more than twice as long as wide and bearing apical bristles; body of claspette with short subapical bristles 4
Claspette without distinct apical fingerlike cylindrical process, apical bristle borne on a short broad conical process; body of claspette with several strong subapical bristles borne on similar but smaller tubercles 5
- 4(3). Apex of aedeagus deeply emarginate in dorsal aspect producing lateral lobes and/or distal half of aedeagus distinctly broader than proximal half; basal tergal bristles of sidepiece strong, subequal in length and development to tergomesal marginal bristles 16. *busckii*
Aedeagus not emarginate apically in dorsal aspect and roughly of uniform width; basal tergal bristles of sidepiece weak, much shorter and weaker than tergomesal marginal bristles
. 8. *aurites*; 9. *grabhami*; 10. *inaequalis*; 11. *stenei*
- 5(3). Clasper more than 0.5 of sidepiece length, without distinct subapical setae
. 6. *walkeri*
Clasper less than 0.5 of sidepiece length, with distinct subapical setae 6

- 6(5). Clasper gradually tapered to distal 0.75 13. *cozumelensis*
Clasper swollen on base, abruptly tapered at about middle . . . 12. *ioliota*

PUPAE

(7. *argyrites* unknown)

Walker Group

1. Paddle deeply emarginate at hair 1 6. *walkeri*
Paddle usually smoothly rounded on apex, at most shallowly emarginate at
hair 1 2
2(1). Hair 10-C usually at least 10-branched (Aurites Group) 3
Hair 10-C usually less than 5-branched. 6

Aurites Group

- 3(2). Pigmentation very light and uniform; metanotum uniformly lightly pigmen-
ted 4
Pigmentation moderate and uneven; metanotum with light area in the middle
of lateral surface 5
4(3). Hair 2-VI distinctly laterad of hair 3. 8. *aurites*
Hair 2-VI mesad or at level of hair 3. 9. *grabhami*
5(3). Median tergal darkening of abdominal segment III indistinct.
. 10. *inaequalis*
Median tergal darkening of abdominal segment III sharply marked . . .
. 11. *stenei*
6(2). Hair 5-C at least 2.0 of hair 4 (Ioliota Group) 7
Hair 5-C subequal to hair 4 (Albonotatus and Busckii Groups). 8

Ioliota Group

- 7(6). Hair 1-II strongly dendritic and with many branches; paddle ovoid, length
about 1.5 greatest width 12. *ioliota*
Hair 1-II with 7-12 simple branches; paddle rounded, length about 1.2 great-
est width 13. *cozumelensis*

Albonotatus and Busckii Groups

- 8(6). Hairs 7,10-C both single; paddle elongate, length more than 1.5 greatest
width 14. *albonotatus*
Hairs 7,10-C usually at least double; paddle length moderate, usually less
than 1.3 greatest width. 9
9(8). Pinna very long, more than 0.33 of total trumpet length; paddle slightly
emarginate at hair 1; hair 6-III,IV strong, usually at least double . . .
. 15. *bahamensis*
Pinna moderate, about 0.25 of total trumpet length; paddle evenly rounded
on apex; hair 6-III,IV weak, single 16. *busckii*

LARVAE

(7. *argyrites* unknown)

Walker Group

1. Abdominal integument densely covered with large dark-branched spicules 6. *walkeri*
Abdominal integument glabrous at 100X. 2
- 2(1). Hair 13-P present (Ioliota Group). 3
Hair 13-P absent 4

Ioliota Group

- 3(2). Siphon slightly swollen in middle, index about 2.5; comb scales blunt or rounded apically 12. *ioliota*
Siphon slightly evenly tapered from base, index about 2.0; comb scales pointed apically 13. *cozumelensis*

Busckii Group

- 4(2). Ventral brush with 5 pairs of hairs (comb scales sometimes in 2 to 4 rows; pecten teeth sometimes extending well beyond hair 1-S). . . 16. *busckii*
Ventral brush with 6 pairs of hairs 5
- 5(4). Head hair 6-C usually single or double; pecten teeth short and with basal denticles; siphon index 3.0 or less (Albonotatus Group) 6
Head hair 6-C multiple, usually more than 5-branched; pecten teeth long, slender and without basal denticles; siphon index more than 4.0 (Aurites Group). 7

Albonotatus Group

- 6(5). Anal gills subequal; siphonal hair 1-S adjacent to last pecten tooth . . . 14. *albonotatus*
Anal gills markedly unequal; siphonal hair 1-S well beyond last pecten tooth 15. *bahamensis*

Aurites Group

- 7(5). Hair 2-VII large, stellate, 4-7-branched. 11. *stenei*
Hair 2-VII small, single. 8
- 8(7). Siphon index less than 5.5; anal gills markedly unequal, the small distinctly shorter than saddle 10. *inaequalis*
Siphon index 6.0 or more; anal gills subequal and distinctly longer than saddle 9
- 9(8). Head hair 5-C usually single; 7-C very short, less than 0.25 of antenna, and usually triple 9. *grabhami*
Head hair 5-C usually at least triple; 7-C about 0.5 of antenna and usually 6-branched 8. *aurites*

Walker Group

FEMALES. *Head*: Narrow decumbent scales white. Palpus with apical silvery scales (broken in *argyrites*). *Thorax*: Inner dorsocentral line golden, continuous or dotted; median prescutellar line broad, white or predominantly white; outer dorsocentral line faint, narrow, golden; lateral marginal line broadened to form a conspicuous lateral silvery patch from anterior angle to wing base. Acrostichal bristles not developed on disc. Scutellum predominantly dark scaled, light scales restricted to median lobe. *Ssp* without scales; upper *stp* patch separate, large. *Legs*: Foretarsus completely dark; midtarsus with incomplete or complete basal white ring on segment 1; hindtarsus with moderate basal white rings on segments 1-3 in *walkeri*, at least on 1-2 in *argyrites* (rest broken). *Abdomen*: Basomedian tergal light markings creamy, present on proximal segments.

MALE (*walkeri* only). Palpus with basomedian white scales on segments 4,5. Larger claw of foreleg and midleg with both submedian and basal teeth; smaller claw with basal tooth only.

MALE GENITALIA (*walkeri* only). Claspette with short broad conical tubercle bearing 1 apical bristle. Clasper about 0.6 of sidepiece; minute spicules basally; subapical hairs absent. Aedeagus subquadrate, shorter than proctiger, without apical lobes.

PUPA (*walkeri* only). *Cephalothorax*: Hair 5-C usually at least triple, moderately long, subequal to distance from its alveolus to trumpet base and at least 2.0 as long as hair 4; hair 7-C usually 3-branched; hair 10-C with 2-7 branches. *Abdomen*: All large hairs except 1-II,III, 9-VII,VIII usually single or double; hair 2-II laterad of or in line with hair 3; hair 5-IV,V usually extending to apex of tergite following; hair 9-II-VI usually at level or slightly cephalad of hair 6; 9-VII subequal to hair 6-VII; hair 4-VIII single. *Paddle*: Short; apex distinctly emarginate; marginal spicules distinct.

LARVA (*walkeri* only). *Head*: Hair 1-C always branched, usually triple; 4-C unusually long, multiple; 5-C single, long and stout; 6-C usually 4-branched; hairs 11, 12,14-C all stellate, 11-C with unequal branches; 15-C double, long, exceeding apex of mental plate. *Antenna*: Shaft with scattered, short, sharp spicules; hair 1-A single. *Thorax*: Hair 13-P absent. Hairs 0,1,3,4,8,14-P, 1,13,14-M, 1,3,4,5,8,13-T all strongly stellate, with numerous branches, very darkly pigmented; hairs 1-M,T far mesad of hairs 2,3. *Abdomen*: Integument with numerous very dark, large branched spicules; hairs 2 and 9 removed cephalad of hair 8. Hairs 1,2,5,9,13-I-VI, 11-I, 7-II-VI all strongly stellate as on thorax; hair 8-VII cephalodorsad of 9-VII. *Segment VIII*: Comb scales in a single row; individual scale long, pointed and fringed to apex. *Siphon*: Index less than 3.0; integument with rows of short spicules; acus absent, no indication of basal indentation. Pecten extending almost to apex; teeth long, proximal ones simple, distal branched apically. *Anal Segment*: Saddle body with numerous strong spicules; caudal margin with long fringed spines; hair 1-X multiple, near lower end of caudal margin. Ventral brush with 6 pairs of hairs on very strongly sclerotized boss without distinct grid bars.

DISCUSSION. The diagnosis of the group is based almost entirely on *walkeri*, the type species of the subgenus and a common species endemic to Jamaica. *A. argyrites*, known only by the imperfect female holotype from northern Venezuela and possibly a male genitalia slide, is extremely similar to *walkeri* in adult ornamentation and is undoubtedly a member of this group.

The Walker Group possesses many features unique in the section, particularly in the immature stages which are readily recognized from all other species in the sub-

genus. However, the mesonotal pattern of the adults suggests a greater affinity with the Aurites Group than with any other group. As indicated under the latter, this is interpreted here as an indication of introgression with the Sexlineatus Section.

The widely disjunct distribution of the 2 members of the Walkeri Group parallels that of the 2 members of the Ioliota Group and is similarly interpreted as a relict pattern of a group originally with a wide distribution in the central Caribbean area (fig. 3).

The group may be primarily a breeder in bromeliads as is the case with *walkeri* but since the latter sometimes uses treeholes it is possible that these may have been the original breeding sites, perhaps still retained by *argyrates*.

6. *Aedes* (Howardina) *walkeri* (Theobald)

Figs. 3, 7, 8, 16-18

1901. *Culex walkeri* Theobald, 1901:424. TYPE: Holotype ♀ (45/110), Jamaica, date and collector not specified [BM].

Aedes (Howardina) *walkeri* of Bonne and Bonne-Wepster (1925:368); Dyar (1928:235); Edwards (1932:156); Lane (1939:101; 1953:725-726); Horsfall (1955:471); Stone, Knight and Starcke (1959:174); Belkin, Schick and Heinemann (1965:31); Forattini (1965:399,400); Porter (1967:38).

Aedes walkeri of Dyar and Knab (1906b:189,192); Howard, Dyar and Knab (1912:70; 1917:849-852); Picado (1913:325); Dyar (1918:73,80); Johnson (1919:424); Gowdey (1926:74); Thompson (1947:78); Hill and Hill (1948:46).

Howardina walkeri of Theobald (1903a:287-289); Dyar (1905a:49; 1905b:23; 1905c:27-28); Theobald and Grabham (1905:20-22); Theobald (1905:9; 1907:215-216; 1910:220); Coquillett (1906b:26); Grabham (1906:170-171); Surcouf and Gonzalez-Rincones (1911:139-140).

Culex walkeri of Blanchard (1905:416).

Haemagogus walkeri of Dyar and Knab (1906a:166).

FEMALE (fig.16). Wing: 2.62 mm. Proboscis: 2.1 mm. Forefemur: 1.75 mm. Abdomen: about 2.45 mm. As described for group, with the following apparently diagnostic features. *Head*: Median stripe on vertex broad, silvery; light scales on sides and venter creamy. *Thorax* (figs.8,16): Scales on anterior promontory golden. Inner dorsocentral line distinct, continuous and moderately broad; median prescutellar line usually silvery, sometimes with a few golden scales, rarely predominantly golden; outer dorsocentral line golden; lateral marginal line very broad, silvery. Antealar area above paratergite with silvery scales. Silvery scales on median scutellar lobe narrow; lateral lobes with narrow dark scales. Pleural scales as in the group. *Legs*: Forefemur and midfemur predominantly dark anteriorly, a few basal scales creamy, proximal 0.5 of posterior surface broadly creamy, extending distally as a light line, rest dark; hindfemur mostly creamy except for lateral distal dark scales. Midtarsal segment 1 with only a few white scales at base. *Haltere*: Stem pale, knob mostly dark, fringe scales creamy white. *Abdomen*: Basomedian tergal creamy patches distinct on III-VII, a few pale scales on II. Sternites creamy on II-IV, rest of segments with basal creamy and apical dark scales.

MALE (fig.16). Wing: 2.28 mm. Proboscis: 1.93 mm. Forefemur: 1.04 mm. Essentially similar to female in color.

MALE GENITALIA (fig.17). As figured; diagnostic characters as in the key. Ninth tergite lobe indistinct, with 3,4 strong setae. Sidepiece about 2.5 times median width.

Clasper with minute spicules basally; spiniform about 0.2 of clasper.

PUPA (fig.17). Abdomen: 2.7 mm. Trumpet: 0.38 mm; index about 4.5-5.0. Paddle: 0.46 mm. Chaetotaxy as figured; hairs moderately to darkly pigmented. Diagnostic characters as in the key. Readily separated from all other species of the subgenus by the presence of minute denticles on abdomen and by the distinctly emarginate paddle. *Cephalothorax*: Mesonotum moderately pigmented between trumpets, slightly deeper laterally; trumpets contrasting. Hair 1(1), 2(2, 2-3), 3(1, 1-2), 4(3, 2-5), 5(5, 3-6), 6(1, 1-2), 7(3, 2-4), 8(3, 1-5), 9(1), 10(5, 2-7), 11(1, 1-2), 12(3, 2-5). *Abdomen*: Tergite I moderately to strongly pigmented except for usual membranous areas; remaining segments moderately to strongly pigmented, progressively lighter caudad; integument with minute denticles. Segment I: hair 1(8-12 primary branches, each with many secondary branches), 2(1, 1-2), 3(1), 4(3, 2-5), 5(4, 3-6), 6(1, 1-2), 7(2, 1-3), 9(1, 1-2). Segment II: hair 0(1), 1(8, 5-17), 2(1), 3(1), 4(2, 2-4), 5(2, 1-3), 6(1, 1-2), 7(3, 1-4), 8(1, present in some), 9(1). Segment III: hair 0(1), 1(4, 2-9), 2(1, 1-2), 3(1), 4(2, 1-3), 5(2, 1-3), 6(1), 7(2, 2-5), 8(3, 2-5), 9(1), 10(1, 1-2), 11(1), 14(1). Segment IV: hair 0(1), 1(3, 2-4), 2(1, 1-3), 3(3, 2-6), 4(2, 1-2), 5(2, 2-3), 6(1, 1-2), 7(2, 1-4), 8(2, 2-3), 9(1), 10(1, 1-3), 11(1), 14(1). Segment V: hair 0(1), 1(2, 1-3), 2(1, 1-3), 3(1, 1-3), 4(1, 1-5), 5(2, 2-4), 6(1, 1-2), 7(2, 2-5), 8(2, 2-4), 9(1), 10(1, 1-2), 11(1), 14(1). Segment VI: hair 0(1), 1(1, 1-3), 2(1, 1-3), 3(1, 1-2), 4(2, 1-4), 5(3, 2-4), 6(1, 1-2), 7(2, 1-3), 8(2, 2-3), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1, 1-3), 2(1, 1-3), 3(2, 1-3), 4(1, 1-2), 5(2, 1-4), 6(5, 3-6), 7(1, 1-2), 8(2, 2-6), 9(6, 6-9), 10(1), 11(1, 1-4), 14(1). Segment VIII: hair 0(1), 4(1), 9(12, 11-16), 14(1, 1-2). *Paddle*: Uniformly lightly pigmented, midrib slightly darker; dorsal surface with fine denticles, external margin serrated; apex deeply emarginate; hair 1-P slender. Male genital lobe extending to 0.5 of paddle, female genital lobe to 0.41.

LARVA (fig.18). Head: 0.7 mm. Siphon: 0.43 mm. Anal Saddle: 0.22 mm. Chaetotaxy as figured; hairs darkly pigmented. Diagnostic characters as in the key. Readily differentiated from all other species of the subgenus by: (1) stellate hairs with numerous branches, (2) dendritic spicules on abdomen and (3) pecten teeth extending almost to apex of siphon. *Head*: Width subequal to length; integument smooth and strongly pigmented. Mental plate with 12 distinct teeth on each side of strong median tooth, often a smaller detached tooth at base. Hair 0(1), 1(3, 2-3), 3(1), 4(6, 5-8), 5(1), 6(4, 2-5), 7(4, 3-5), 8(1), 9(2), 10(1), 11(14, 9-17; stellate, branches of 3 lengths), 12(10, 8-17), 13(1), 14(15, 11-24; stellate), 15(2, 1-3). *Antenna*: Length about 0.3 of head; uniformly strongly pigmented; with scattered spicules; all hairs usually single; hair 1-A about 0.62 from base. *Thorax*: Integument glabrous; in life thorax appears bluish green. Apex of long hairs attenuate; stellate hairs with numerous branches; long and stellate hairs weakly barbed. Prothorax: hair 0(32, 30-46), 1(32, 27-38), 2(1), 3(26, 24-36), 4(36, 30-42), 5(4, 3-5), 6(1, 1-2), 7(3, 2-4), 8(36, 30-38), 9(2, 1-4), 10(1), 11(4, 3-5), 12(1), 14(48, 44-54). Mesothorax: hair 1(36, 25-54), 2(1), 3(1), 4(1), 5(1), 6(8, 5-8), 7(1), 8(8, 7-10), 9(10, 7-14), 10(1), 11(3, 2-4), 12(1), 13(22, 17-27), 14(23, 19-29). Metathorax: hair 1(54, 48-63), 2(1), 3(22, 19-24), 4(28, 28-34), 5(25, 22-33), 6(1), 7(8, 7-10), 8(19, 16-23), 9(8, 6-8), 10(1, 1-2), 11(3, 2-4), 12(1), 13(42, 38-43). *Abdomen*: Integument densely packed with large dendritically branched spicules, more sparsely on segment I; stellate hairs as on thorax. Segment I: hair 1(53, 51-71), 2(40, 40-53), 3(1), 4(2, 1-2), 5(29, 28-41), 6(3, 3-4), 7(1, 1-2), 9(14, 9-15), 10(1), 11(26, 24-30), 13(35, 29-38). Segment II: hair 0(1), 1(60, 52-65), 2(46, 36-46), 3(1), 4(2, 1-3), 5(32, 25-36), 6(4, 3-4), 7(18, 14-22), 8(1), 9(20, 18-22), 10(1), 11(1), 12(1), 13(36, 33-44). Segment III: hair 0(1), 1(64, 56-66), 2(41, 35-45), 3(1), 4(1), 5(34, 30-40), 6(3, 2-3), 7(20, 20-24), 8(1),

9(21, 21-26), 10(1), 11(1), 12(1), 13(36, 32-44), 14(1). Segment IV: hair 0(1), 1(60, 54-62), 2(42, 36-46), 3(1), 4(1, 1-2), 5(37, 30-42), 6(2, 2-3), 7(20, 18-22), 8(1), 9(24, 22-27), 10(1), 11(1), 12(1), 13(40, 25-41), 14(1). Segment V: hair 0(1), 1(60, 47-61), 2(37, 37-42), 3(1), 4(3, 1-3), 5(36, 30-41), 6(2, 2-3), 7(20, 18-25), 8(1), 9(26, 25-31), 10(1), 11(1), 12(1), 13(36, 30-42), 14(1, 1-2). Segment VI: hair 0(1), 1(56, 44-60), 2(41, 36-41), 3(1), 4(2, 1-2), 5(30, 30-42), 6(2, 1-2), 7(22, 18-24), 8(1), 9(28, 25-29), 10(1), 11(1), 12(1), 13(34, 28-38), 14(1). Segment VII: hair 0(1), 1(50, 42-50), 2(36, 30-40), 3(1), 4(1), 5(28, 28-39), 6(20, 16-26), 7(1), 8(24, 22-28), 9(26, 26-32), 10(1), 11(1), 12(1), 13(22, 20-28), 14(2). *Segment VIII*: Comb scales in a single row of 12(10-14); individual scales long, pointed apically, fringed to the tip. Hair 0(1), 1(48, 46-54), 2(1), 3(8, 8-10), 4(1), 5(28, 26-31), 14(2, 1-2). *Siphon*: Index about 2.8-2.9; darkly pigmented; integument uniformly pilose. Pecten extending beyond hair 1-S, almost to apex; 20(16, 22) teeth, progressively longer distad, individual teeth long, without basal denticles, distal teeth broad, with apical denticles. Hair 1-S about 0.67 from base. Hair 1(3, 2-4), 2(1), 3-5 not visible, 6(1), 7(1), 8(1), 9(1). *Anal Segment*: Saddle strongly pigmented, with darker basal ring; integumentary spicules progressively larger distally; caudal margin with long spines fringed laterally. Gills narrow, moderately long, ventral pair slightly shorter than dorsal. Hair 1(8, 6-10; strong, at caudolateral angle), 2(12, 10-14), 3(1), 4a(7, 6-8), 4b(7, 6-7), 4c(6, 5-8), 4d(6, 6-7), 4e(6, 6-7), 4f(5, 4-7).

EGG. Length about 0.62 mm, width about 0.14 mm; exochorion transparent and endochorion dark and with polygonal sculpturing.

SYSTEMATICS. *A. walkeri*, the type species of *Howardina*, is among the most clearly marked species in the subgenus. In the adults, only the closely related *argyrites*, known by a single female from Venezuela, could be confused with *walkeri*. The immature stages are also very strikingly differentiated but it would not be surprising if those of *argyrites*, when found, were to conform to the same general type in view of the resemblance of the females.

Little variation is apparent in the extensive material of *walkeri*, either in the adults or the immature stages. Only the median prescutellar line exhibits some noticeable variation, ranging from entirely silvery in the majority of specimens to predominantly golden in a few. The dorsocentral lines are always clearly marked and never dotted as in *argyrites*.

BIONOMICS. The breeding sites of *walkeri* are usually bromeliad axils but a few collections of immatures have been made in treeholes (JA 336,390), broken and cut bamboo (JA 711,778), heliconia axils (JA 748) and a crabhole (JA 369). Both terrestrial and arboreal bromeliads are used by *walkeri*. This species has been found associated with all members of the Aurites Group and appears to have a much wider altitudinal and geographical range than any other species of *Howardina* on Jamaica. The larvae of *walkeri* are readily recognized in the field by their very dark and "hairy" bodies.

Females of *walkeri* commonly bite humans under the shade of bromeliad laden trees. I found a maximum peak of activity in mid morning (0900) and a lesser one in late afternoon (1700) as shown in fig.7. However, Hill and Hill (1948:46) state that *walkeri* prefers to feed at dusk in the open, and bites at any time of the day in forest shade.

DISTRIBUTION (fig.3). Endemic to the island of Jamaica where it is widespread at elevations from 100 ft to 4500 ft. Material examined: 2964 specimens; 244 ♂, 1139 ♀, 699 pupae, 882 larvae; 516 individual rearings (237 pupal, 150 larval, 129 incomplete).

JAMAICA. *Clarendon*: Honeycomb Rock, elev. 800 ft, 8 Aug 1965, W.A. Page (JA 237), 1 lp (237-27) [UCLA]. Mocho Road, 10 Sept 1965, J.N. Belkin, 1 ♀ (JA 353) [UCLA]. Slippery Fall, elev. 800 ft, 8 Aug 1965, W.A. Page, 1 L (JA 239) [UCLA]. *Hanover*: Copse, elev. 500 ft, 6 Nov 1966, O.G.W. Berlin and D.C. Watson (JA 668), 1 p♂ (668-101), 1 p♀ (668-100), 6 L, 2 l [UCLA]. Lethe, elev. 500 ft, 6 Nov 1966, O.G.W. Berlin and D.C. Watson, 4 p, 1 L, 5 l (JA 655), 1 lp♀ (667-10), 5 p♂ (667-100-104), 5 lP (667-11-15), 2 ♀, 2 P, 4 p, 34 L, 4 l (JA 667) [UCLA]. *Manchester*: Hope Farm, elev. 1000-1100 ft, 10 Sept 1965, W.A. Page, 1 p♀ (354-102), 1 lP (354-13), 55 ♀ (JA 356); 23 Oct 1966, O.G.W. Berlin and D.C. Watson, 31 ♀ (JA 634A), 2 lp♂ (635-11,16), 2 lp♀ (635-10,12), 4 p♂ (635-100-103), 1 p♀ (635-104), 8 lP (635-13-15,17-21), 1 P, 2 l (JA 635); 2 Nov 1966, O.G.W. Berlin, 12 ♀ (JA 663A), 779 ♀ (JA 684) [UCLA]. Mandeville, elev. 900 ft, 23 Oct 1966, O.G.W. Berlin and D.C. Watson (JA 639), 4 lp♀ (639-10,14,22,25), 8 p♂ (639-101,104,107-111,114), 7 p♀ (639-100-103,105,106,112,113), 12 lP (639-11-13,15-21,23,24), 9 ♂, 4 ♀, 18 P, 22 p, 62 L, 24 l; 24 Oct 1966, O.G.W. Berlin (JA 640), 1 lP (640-10), 1 L [UCLA]. Melrose Hills, elev. 900 ft, 8 Aug 1965, W.A. Page (JA 244), 1 lp♂ (244-43), 1 p♀ (244-41A), 1 lP (244-40), 7 P [UCLA]. Porus, elev. 900-1000 ft, 8 Aug 1965, W.A. Page (JA 243), 2 lp♂ (243-22,29), 3 lp♀ (243-21,26,27), 1 p♂ (243-102), 2 p♀ (243-101,103), 2 lP (243-19,20), 1 P, 15 L; 23 Oct 1966, O.G.W. Berlin and D.C. Watson, 1 lP (631-30), 2 lp♀ (633-11,12), 1 p♀ (633-100), 5 lP (633-10,13-16), 4 L (JA 633); 1 Nov 1966, O.G.W. Berlin (JA 657), 2 lp♂ (657-10,11), 1 p♂ (657-100), 2 p♀ (657-101,102), 2 lP (657-13,14), 2 P, 2 p, 1 L, 7 l; 2 Nov 1966, O.G.W. Berlin, 1 lp♂ (660-10), 1 p♂ (660-100), 1 P (JA 660), 1 lp♀ (664-12), 4 p♂ (664-100,103-105), 2 p♀ (664-101,102), 2 lP (664-10,11), 1 P, 22 L (JA 664) [UCLA]. Williamsfield, elev. 1100 ft, 23 Oct 1966, O.G.W. Berlin and D.C. Watson (JA 637), 4 lp♂ (637-10,11,13,17), 3 lp♀ (637-12,23,27), 10 p♂ (637-100-105,108-110,112), 3 p♀ (637-106,107,111), 11 lP (637-14-16,18-22,24-26), 3 p, 25 L, 1 l [UCLA]. *Portland*: Ecclesdown, elev. 1000 ft, 22 Aug 1967, J.N. Belkin and W.A. Page (JA 748), 1 p♀ (748-94), 1 p [UCLA]. Fairy Hill, elev. 100 ft, 13 Nov 1966, O.G.W. Berlin and D.C. Watson, 20 L, 2 l (JA 693), 4 lp♂ (694-11,13,14,17), 9 lp♀ (694-10,12,15,18-23), 21 p♂ (694-100-103,106-108,112-117,119-121,123,125,128-131), 13 p♀ (694-101,104,105,109-111,118,122,124,126,132,133), 1 lP (694-16), 4 ♂, 1 ♀, 2 P, 2 p, 34 L (JA 694), 19 L (JA 695) [UCLA]. Kemney-Sherwood Forest, elev. 750 ft, 13 Aug 1967, J.N. Belkin and W.A. Page (JA 707), 3 lp♂ (707-10-12), 2 p♂ (707-100,102), 1 lP (707-13), 1 P, 1 L; 13 Aug 1967, W.A. Page, 2 lp♂ (708-11,12), 1 lp♀ (708-15), 1 ♂ (JA 708), 1 lp♂ (709-10), 1 p♂ (709-101), 1 p, 1 L (JA 709), 1 L (JA 710), 1 lp♂ (716-10), 3 p♂ (716-100,101,104), 1 P, 4 L (JA 716) [UCLA]. Portland Point, 4 Aug 1942, C.B. Philip, 1 ♀ [USNM]. *St. Andrew and Kingston*: Castleton, elev. 600 ft, 27 Oct 1966, O.G.W. Berlin and D.C. Watson (JA 645), 2 lP (645-10,11), 1 P, 5 L, 5 l [UCLA]. Duhaney River, 6 Nov 1965, W.A. Page (JA 399), 1 lP (399-13) [UCLA]. Ferry Quarry, 13 Sept 1965, W.A. Page, 1 ♂ (JA 369) [UCLA]. Hardwar Gap, elev. 3800 ft, 29 Oct 1966, O.G.W. Berlin (JA 647), 2 lp♂ (647-10,11), 1 lp♀ (647-12), 1 p♂ (647-100), 1 p♀ (647-101), 1 P, 1 p, 1 L, 1 l [UCLA]. Hermitage Dam, 1934, 6 ♀ [USNM]. Hermitage Dam Road, 22 Aug 1965, W.A. Page (JA 282), 1 lp♂ (282-36), 1 lp♀ (282-33), 1 lP (282-31); 13 Aug 1965, W.A. Page, 1 lP (294-44), 1 lP (304-21); 1 Sept 1965, W.A. Page, 1 lp♂ (319-22), 1 lp♀ (319-23), 1 p♂ (319-104), 31 L (JA 319), 1 lp♀ (322-23), 3 lP (322-24,31,32), 1 ♀ (JA 322), 3 L (JA 323), 2 p♀ (324-102,103), 6 L (JA 324); 7 Sept 1965, J.N. Belkin (JA 333), 1 lp♀ (333-21), 1 p♂ (333-100), 2 p♀ (333-101,102), 1 lP (333-20), 2 L; 29 Oct 1965, W.A. Page, 1 ♀ (JA 390), 1 P (JA 391), 1 lp♂ (392-12), 1 lp♀ (392-11), 6 p♂ (392-102,104,106,109,111,113), 4 p♀ (392-100,101,105,114), 1 lP (392-10), 2 ♂, 2 ♀, 2 p, 16 L (JA 392), 1 lp♂ (393-12); 15 Aug 1967, J.N. Belkin and W.A. Page, 1 lp♀ (723-30), 1 p♂ (723-103), 1 p♀ (723-102), 2 L (JA 723), 2 lp♂ (724-12,14), 3 lp♀ (724-10,11,15), 3 p♂ (724-102-104), 1 lP (724-13), 1 P, 2 p, 3 L (JA 724), 2 lp♂ (725-15,16), 1 lp♀ (725-14), 5 p♂ (725-90,100A,105A,106,108A), 3 p♀ (725-92,107,112), 3 ♂, 3 ♀, 1 P, 3 p (JA 725); 1 Sept 1967, W.A. Page and J.N. Belkin (JA 765), 1 lP (765-10), 2 L; 13 July 1967, W.A. Page (JA 843), 3 lp♂ (843-12,13,15), 3 lp♀ (843-10,11,14), 1 p♂ (843-101), 2 p♀ (843-100,102); 25 July 1967, W.A. Page, 1 L (JA 854), 1 lp♂ (855-11), 2 lp♀ (855-10,12), 3 lP (855-13-15), 1 P, 6 L (JA 855) [UCLA]. Kingston, 1 Apr 1906, M. Grabham, 1 ♂, 2 ♀ [USNM]. Mavis Bank, M. Grabham, 1 ♂ [USNM]. Mt. Salus Road, elev. 1500 ft, 11 Sept 1967, W.A. Page, 1 p♂ (777-100), 2 lP (777-10,11), 1 lp♂ (779-10), 1 p♂ (779-104), 2 p♀ (779-101,105), 1 ♀, 1 P, 2 L (JA 779); 24 July 1967, W.A. Page (JA 848), 1 lP (848-10), 1 P, 1 L, 1 l [UCLA]. Newcastle,

elev. 2500-4000 ft, 5 Sept 1964, W.A. Page (JA 124), 1 lp♂ (124-15), 3 lp♀ (124-10,12,14), 1 IP (124-11), 2 L; 29 Oct 1966, O.G.W. Berlin (JA 648), 1 lp♂ (648-16), 1 lp♀ (648-19), 2 p♂ (648-100,101), 9 IP (648-10-15,17,18,20), 1 P, 9 L, 13 l; track to Catherines Peak, elev. 4000-4300 ft, 8 Nov 1966, O.G.W. Berlin, 1 P, 1 p, 1 L, 1 l (JA 678), 9 ♀ (JA 679), 2 p♀ (680-100,101), 1 ♀, 2 P, 1 p, 2 L (JA 680), 1 p, 2 L, 5 l (JA 681), 1 P, 16 L (JA 682), 1 P, 1 L, 1 l (JA 683) [UCLA]. Stony Hill, elev. 1100 ft, 18 July 1964, L. Paton (JA 85), 3 p♂ (85-101,103,104), 8 p♀ (85-100,102,105-108,110,111), 1 P, 3 L; 1 Sept 1965, W.A. Page (JA 318), 2 lp♂ (318-32,35), 1 lp♀ (318-38), 5 p♂ (318-33,34,110,111,113), 6 p♀ (318-102,104,106-109), 1 IP (318-36), 1 ♂, 8 P, 1 p, 5 L [UCLA]; 1934, 3 ♀ [USNM]. Uester Road, elev. 4500 ft, 8 Sept 1965, J.N. Belkin, 1 ♀ (JA 336), 5 lp♂ (337-10,14,15,18,24), 2 lp♀ (337-11,16), 2 p♂ (337-22,23), 1 p♀ (337-27), 1 IP (337-17), 5 ♂, 3 ♀, 1 P, 4 L (JA 337) [UCLA]. Waterworks track, elev. 1100 ft, 8 Sept 1965, J.N. Belkin (JA 335), 2 lp♂ (335-10,20), 3 lp♀ (335-11,22,30), 1 p♂ (335-100), 1 IP (335-25), 8 ♂, 2 ♀, 2 p, 6 L [UCLA]. Woodcutters Gap, elev. 4500 ft, 3 Sept 1964, W.A. Page (JA 122), 1 lp♀ (122-11), 2 ♂ (JA 122), 1 lp♂ (123-10), 1 lp♀ (123-11), 1 p♂ (123-100) [UCLA]. *St. Ann*: Moneague, elev. 500-1750 ft, 9 Sept 1965, D.C. Watson, 2 p♀ (606-100,101), 4 IP (606-10-13), 4 L (JA 606), 1 ♀ (JA 607); 17 Aug 1967, J.N. Belkin and W.A. Page, 2 L (JA 733); 31 Aug 1967, W.A. Page, 2 L (JA 762); 2.0 mi S of Moneague near Unity, elev. 1750 ft, 28 Aug 1967, W.A. Page (JA 758), 1 lp♂ (758-22), 1 lp♀ (758-21), 1 p♂ (758-102), 1 IP (758-20); 29.0 mi post on Moneague Road, elev. 1750 ft, 30 Aug 1967, W.A. Page, 5 lp♂ (763-10,11,13,15,17), 1 lp♀ (763-16), 1 p♂ (763-91), 4 p♀ (763-93,104,110,113), 3 ♂, 1 ♀, 3 p, 4 L, 1 l (JA 763), 2 lp♀ (764-11,20), 2 L (JA 764); Moneague-Claremont Road, elev. 750-1250 ft, 17 Sept 1965, W.A. Page, 1 ♂ (374-100), 1 lp♂ (379-12), 2 lp♀ (379-10,14), 1 IP (379-11), 4 L (JA 379), 1 l (JA 381); 5 Aug 1967, W.A. Page, 1 p (JA 767) [UCLA]. *St. James*: Montego Bay, elev. 500 ft, 6 Nov 1966, O.G.W. Berlin and D.C. Watson (JA 669), 1 p♀ (669-103), 1 IP (669-20), 2 L [UCLA]; Jan 1940, W.H.W. Komp, 2 l [USNM]. Reading, elev. 200 ft, 6 Nov 1966, O.G.W. Berlin, 1 l (JA 670), 1 l (JA 671), 2 ♀ (JA 672) [UCLA]. *St. Mary*: Broadgate, elev. 500 ft, 25 Aug 1965, D.C. Watson, 1 L (JA 257); 27 Oct 1966, O.G.W. Berlin and D.C. Watson (JA 643), 2 lp♂ (643-10,14), 4 lp♀ (643-11-13,15), 1 p♂ (643-109), 2 p♀ (643-110,111), 1 IP (643-16), 2 p, 1 L, 8 l [UCLA]. Castleton, elev. 600 ft, 27 Oct 1966, O.G.W. Berlin and D.C. Watson (JA 644), 1 lp♀ (644-20), 1 p♀ (644-110), 6 P, 4 L [UCLA]. *St. Thomas*: Barrett's Gap, 14 Nov 1946, G.A. Thompson, 1 ♀ [IJ]. Norris, elev. 500 ft, 30 Oct 1966, O.G.W. Berlin and D.C. Watson (JA 653), 1 lp♀ (653-21), 1 p♀ (653-100), 2 IP (653-20,22), 1 P, 4 p, 1 L, 1 l [UCLA]. Pleasant Hill, elev. 250 ft, 14 June 1931, Kisliuk, 7 ♀ [USNM]. Port Morant Bay, 16 Aug 1967, J.N. Belkin and W.A. Page, 2 ♂, 1 L (JA 729) [UCLA]. Scotland Gate, elev. 500 ft, 30 Oct 1966, O.G.W. Berlin and D.C. Watson (JA 654), 5 p♂ (654-100,102,103,107,109), 5 p♀ (101,104-106,108), 10 IP (654-10-19), 1 ♀, 10 P, 10 l [UCLA]. Windsor Forest, elev. 750 ft, 30 Oct 1966, O.G.W. Berlin and D.C. Watson, 1 lp♂ (650-10), 1 p♂ (650-113), 1 p♀ (650-103), 4 IP (650-12-15), 1 P, 1 L, 2 l (JA 650), 4 lp♂ (651-10,11,14,15), 5 lp♀ (651-12,17,19-21), 7 p♂ (651-100-102,105-108), 5 p♀ (651-103,104,109,115,116), 3 IP (651-13,16,18), 4 P, 1 p, 6 L, 1 l (JA 651) [UCLA]. *Westmoreland*: Whitehouse, elev. 100 ft, 11 Sept 1965, W.A. Page, 1 ♀ (JA 359), 3 ♀ (JA 360) [UCLA]. *Parish not specified*: Sandy Folly, Feb 1945, G.A. Thompson, 1 L; Jan 1940, W.H.W. Komp, 1 ♂; 1940, W.H.W. Komp, 1 ♀; Jan 1946, G.A. Thompson, 1 ♂, 9 ♀; 1940, 1 ♀; M. Grabham, 1 ♂, 3 ♀, 1 p, 5 l; R.B. Hill, 3 ♀; G.A. Thompson, 1 ♀ [USNM]; W.A. Page, 1 IP (771-11), 1 lp♂ (772-20), 1 lp♀ (772-21), 3 L, 1 l (JA 772), 2 lp♂ (787-12,14), 2 lp♀ (787-11,13), 3 p♂ (787-108,109,111), 7 p♀ (787-100-102,104,105,107,112), 1 IP (787-10), 1 P, 1 p, 10 L (JA 787) [UCLA].

7. *Aedes* (*Howardina*) *argyrites* Dyar and Nunez Tovar

Figs. 3, 8

1927. *Aedes* (*Howardina*) *argyrites* Dyar and Nunez Tovar, 1927:190. TYPE: Holotype ♀, Venezuela, M. Nunez Tovar [USNM].

Aedes (*Howardina*) *argyrites* of Dyar (1928:230); Edwards (1932:155); Lane (1939:99); Anduze (1941:14); Lane (1953:708); Horsfall (1955:471); Stone and Knight (1956:226); Stone, Knight

and Starcke (1959:173); Belkin, Schick and Heinemann (1965:74); Cova Garcia, Sutil and Rausseo (1966a:58; 1966b:141,333).

FEMALE. Apparently distinct from *walkeri* in the following features (fig.8). Sides and venter of head mottled with black and white scales; inner dorsocentral mesonotal line faint, narrow, dotted; midtarsal segment 1 with complete basal ring. The single known specimen has the apex of the proboscis, palpi, antennae and segments 3-5 of hindtarsi broken; hindtarsal segments 1 and 2 have basal white rings.

MALE, PUPA, LARVA unknown.

SYSTEMATICS. The pattern of ornamentation of the single known adult of *argyrites* is so similar to that of *walkeri* that I have no hesitation in assigning *argyrites* to the Walkeri Group. The 2 forms are apparently differentiated primarily by the diagnostic characters given above but since the holotype of *argyrites* is damaged it is possible that additional differences may be present, especially in tarsal markings. A slide of male genitalia [USNM] from an unspecified locality in Venezuela (P.J. Anduze) probably represents another specimen of *argyrites*, as identified by W.H.W. Komp. There appear to be some differences between these and the male genitalia of *walkeri* but without additional material and the absence of the whole adult I hesitate to describe them at this time.

The exact type locality of *argyrites* is not known but the most likely place is somewhere in the Cordillera de la Costa in the state of Aragua, the origin of the bulk of the material collected by Nunez Tovar. Failure to find additional material of *argyrites* in this relatively well-known area suggests that *argyrites* may be a rare relict form.

BIONOMICS. The holotype was presumably obtained in a biting-landing collection. Immature stages of *argyrites* should be looked for in bromeliad axils, treeholes and broken bamboo, the known breeding sites of the closely related *walkeri*.

Aurites Group

FEMALES. *Head:* Narrow decumbent scales yellowish. Palpus with a few white scales on apex. *Thorax:* All light mesonotal lines golden, varied in development; lateral line sometimes moderately to rarely strongly broadened but not silvery. Acrostichal bristles not developed on disc. Scutellum with linear golden scales on lateral lobes. *Ssp* with or without scales; upper *stp* patch separate or united. *Legs:* Foretarsus completely dark; midtarsus with basal white markings on segments 1 or 1,2; hindtarsus with basal white markings on segments 1,2 or 1-3. *Abdomen:* Basomedian tergal light markings when present restricted to distal segments.

MALES. Palpus entirely dark. Larger claw of foreleg and midleg with small acute basal tooth and large submedian tooth; smaller claw with basal tooth only.

MALE GENITALIA. Claspette with a distinct outstanding apical fingerlike cylindrical process more than twice as long as wide and bearing a short apical bristle. Clasper about 0.5 of sidepiece; basal half with minute spicules; subapical hairs absent. Aedeagus subquadrate, slightly wider at middle, subequal to proctiger in length.

PUPAE. *Cephalothorax:* Hair 5-C at least 4-branched, moderately long but usually not reaching base of trumpet; hair 7-C with 3 or more branches; hair 10-C usually at least 10-branched. *Abdomen:* Hair 1-II-IV with many branches, 1-II with about as many branches as float hair (1-I); hair 2-II always mesad of hair 3; hair 5-IV,V usually double and about 1.5 of tergite following; hair 9-II-VI usually at level or slightly

cephalad of hair 6; 9-VII subequal to hair 6-VII; hair 4-VIII double. *Paddle*: Moderate; practically unpigmented; apex rounded; marginal spicules indistinct.

LARVAE. *Head*: Hair 1-C unbranched; 4-C short; 5-C single or branched, long; 6-C at least 6-branched, moderate; none of ventral hairs stellate; 14-C single; 15-C short, not extending cephalad of base of mental plate. *Antenna*: Shaft with a few scattered spicules; hair 1-A spikelike, single. *Thorax*: Hair 13-P absent. Only hairs 0, 1, 3, 14-P and 5-T stellate, with a few, weakly barbed branches; hair 1-T far mesad of 2, 3-T. *Abdomen*: Integument glabrous; all hairs except 0, 8, 14 at about same transverse level. Only hairs 2, 5-I-VI, 11-I, 7-9-II-VI stellate, with a few weakly barbed branches; hairs 2 and 9 stronger than others; 9-I small, single; hair 8-VII distinctly cephalodorsad of 9-VII. *Segment VIII*: Comb scales in a single row; individual scales long and fringed to apex. *Siphon*: Index 5.0-8.5; integument glabrous; acus absent but base of siphon with small lateral indentation. Pecten not reaching middle of siphon; teeth long, without denticles. *Anal Segment*: Saddle body without distinct spicules except distally; caudal margin with row of long spines; hair 1-X always single and at lower end of caudal margin. Ventral brush with 6 pairs of hairs on a weak boss without grid bars.

DISCUSSION. The clearly marked Aurites Group shows a phenomenon unique in the subgenus: a flock of 4 sibling species sympatric in one small area. To date the group has been recognized only in Jamaica, where some of the species are quite common (fig. 3).

There is a suggestion of some affinity of this group with the sympatric Walkeri Group in the general similarity in the mesonotal pattern of the adults. However, the immature stages of the 2 groups are very distinct. There is a much greater resemblance in the mesonotal pattern of the adults with the Sexlineatus Section except for the prescutellar line, and the larvae and pupae also resemble the Sexlineatus Section more than any group in the Walkeri Section. Although this resemblance may be entirely fortuitous, 2 more plausible explanations are possible. First, the Aurites Group might be the primitive stock of the Walkeri Section derived from the Sexlineatus Section; this is very unlikely since the entire Sexlineatus Section lacks several important primitive characters represented in other groups of the Walkeri Section (acrostichal bristles of the adults and comb scales in a patch in the larva). Second, the view held here; the Aurites Group may have been formed through relatively recent introgression between the Sexlineatus Section and the Walkeri Group. This interpretation would also account for the presence of a species flock in the Aurites Group, since such radiation usually takes place soon after a new phyletic line is established. It is also supported indirectly by the presence in Jamaica of several species in other genera that are either identical with or very closely related to Central American species, strongly suggesting a relatively recent connection between these areas.

No specific differences in the male genitalia of members of the group have been found and the adults of *inaequalis* and *stenei* cannot be separated from each other. In other respects the 4 species are readily differentiated from one another as indicated in the keys.

There appear to be some ecological barriers separating 2 of the species. *A. inaequalis* breeds in treeholes, broken bamboo and rockholes, largely at low elevations, and never in bromeliad axils, which are utilized exclusively by the other 3 species. *A. aurites* breeds primarily at elevations above 3,500 feet and has never been found associated with the other bromeliad-breeding members of the group. *A. grabhami* and *stenei* occur primarily below 2,500 feet but *grabhami* has been collected at elevations up to 4,000 feet. These 2 species are usually found associated in collections but it is not known if they occupy the same axils under natural conditions.

8. *Aedes* (Howardina) *aurites* (Theobald)

Figs. 3, 8, 19, 20

1907. *Howardina aurites* Theobald, 1907:216-218. TYPE: Lectotype ♀, Newcastle (St. Andrew), Jamaica, elev. 4000 ft, July 1906, Col. Loscombe [BM; selection of Belkin, 1968].

Aedes (Howardina) *aurites* in part of Dyar (1928:236); Edwards (1932:155); Lane (1939:99; 1953:720-722); Horsfall (1955:471).

Aedes aurites of Howard, Dyar and Knab (1917:859-860); Dyar (1918:73); Johnson (1919:424); Gowdey (1926:73).

Aedes aurites in part of Hill and Hill (1948:29, 42).

Howardina aurites of Theobald (1910:220); Surcouf and Gonzalez-Rincones (1911:139-140).

Aedes (Howardina) *inaequalis* in part of Thompson (1956:199-200); Stone, Knight and Starcke (1959:174); Belkin, Schick and Heinemann (1965:31); Forattini (1965:399, 400).

Aedes inaequalis in part of Stone and Knight (1956:219).

FEMALE. Wing: 2.6 mm. Proboscis: 2.00 mm. Forefemur: 1.8 mm. Abdomen: about 2.7 mm. *Head*: Light decumbent scales golden on median stripe and short orbital line, yellowish on sides and venter. Erect scales yellowish, a few lateral ones darker. Palpus about 0.16 of proboscis. *Thorax* (fig. 8): Mesonotal dark scales dense; light lines golden, moderately broad, wider than dark lines; inner dorsocentral line reaching to prescutellar space, followed by moderately broad median prescutellar line; outer dorsocentral line complete, merging with lateral marginal line anteriorly; lateral marginal line long, extending from side of anterior promontory to wingbase, very broad from scutal angle to wingbase due to presence of golden scales on antealar area above paratergite. Median scutellar lobe with a row of narrow golden scales flanked on sides by broad dark ones; lateral lobes with a few narrow, golden and black scales. *Apn* with a distinct silvery patch; *ssp* bare; patches on base of *pra*, upper and lower *stp* merged and continuous; rest of patches as in the section and group. *Legs*: Forefemur and midfemur predominantly dark anteriorly except for a few basal creamy scales, posterior surface and hindfemur predominantly creamy except for distal dark areas. Midtarsus with few white scales on segment 1; hindtarsus with short white rings on 1, 2, rest dark scaled. *Haltere*: Stem pale, knob predominantly dark, fringe scales whitish. *Abdomen*: Basomedian tergal light scaling inconspicuous. Sternites II-IV straw yellow, V predominantly yellow with few apical dark scales; rest of segments with basal creamy and distal dark scales.

MALE. Wing: 2.34 mm. Proboscis: 2.16 mm. Forefemur: 1.71 mm. Essentially similar to female in coloration.

MALE GENITALIA (fig. 19). As figured; diagnostic characters as in the key. Ninth tergite lobe indistinct, with 2 strong bristles. Sidepiece length about 3.0 median width. Clasper about 0.6 of sidepiece, basal 0.3 with minute spicules; spiniform short, about 0.25 of clasper.

PUPA (fig. 19). Abdomen: 2.48 mm. Trumpet: 0.38 mm; index 6.0-6.2. Paddle: 0.7 mm. Readily separated from *inaequalis* and *stenei* by the absence of lightly pigmented area on metanotum and hair 9-C single; from *grabhami* by hair 2-VI laterad of 3-VI. *Cephalothorax*: Mesonotum and metanotum uniformly lightly pigmented; trumpets contrasting. Hair 1(1), 2(2, 1-2), 3(1, 1-2), 4(5, 3-8), 5(5, 4-7), 6(1, 1-2), 7(4, 4-6), 8(1), 9(1), 10(10, 9-16), 11(1), 12(3, 2-6). *Abdomen*: Tergite I uniformly lightly pigmented except for usual membranous areas; rest of segments light, pigmentation progressively lighter caudad. Segment I: hair 1(12-18 primary branches, each with many secondary ones), 2(1), 3(1), 4(6, 3-8), 5(6, 2-6), 6(1, 1-2), 7(2, 2-3), 9(1),

10(1, present in some). Segment II: hair 0(1), 1(37-56 branches, variable in different specimens), 2(1), 3(1), 4(4, 2-4), 5(1), 6(1), 7(4, 3-4), 9(1), 10(1, present in some). Segment III: hair 0(1), 1(14, 6-24), 2(1), 3(1, 1-3), 4(4, 2-4), 5(1), 6(1), 7(3, 2-4), 8(3, 2-4), 9(1, 1-2), 10(2, 2-3), 11(1), 14(1). Segment IV: hair 0(1), 1(8, 5-16), 2(1, 1-2), 3(4, 3-6), 4(2, 1-4), 5(1, 1-3), 6(1), 7(3, 2-5), 8(2, 1-3), 9(1), 10(2, 2-4), 11(1), 14(1). Segment V: hair 0(1), 1(2, 1-7), 2(1, 1-2), 3(2, 2-3), 4(5, 3-8), 5(1), 6(1), 7(4, 2-6), 8(2, 1-3), 9(1), 10(1, 1-2), 11(1), 14(1). Segment VI: hair 0(1), 1(1, 1-6), 2(1), 3(2, 1-3), 4(4, 2-6), 5(2, 1-5), 6(1, 1-3), 7(1), 8(3, 1-8), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1, 1-2), 4(2, 1-2), 5(1, 1-2), 6(2, 2-4), 7(1, 1-2), 8(3, 2-4), 9(3, 2-4), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(2), 9(10, 8-12), 14(1). *Paddle*: Almost without pigmentation; midrib faintly pigmented; external margin smooth. Male genital lobe extending to 0.42 of paddle, female genital lobe to 0.27.

LARVA (fig.20). Head: 0.73 mm. Siphon: 0.97 mm. Anal Saddle: 0.24 mm. Readily separated from *stenei* by hair 2-VII small and single; from *inaequalis* by the longer subequal gills and at least 3-branched hair 5-C; from *grabhami* by the 3-branched hair 5-C. Chaetotaxy as given below, hairs moderately pigmented. *Head*: Width about 1.18 of length; pigmentation light, deeper around mouthparts and behind ocular area ventrally. Mental plate with a strong median tooth and 10 distinct teeth on either side. Hair 0(1), 1(1), 3(1), 4(4, 4-5), 5(3, 2-4), 6(10, 9-13), 7(6, 4-7), 8(1), 9(3, 2-3), 10(1), 11(3, 3-5), 12(1, 1-2), 13(1), 14(1, small), 15(3, 3-4). *Antenna*: Length about 0.44 of head, very lightly pigmented and with few scattered spicules. All hairs single; hair 1-A about 0.5 from base. *Thorax*: Long hairs attenuate apically and weakly barbed; stellate hairs with a few weakly barbed branches. Prothorax: hair 0(11, 8-14), 1(9, 9-11), 2(1), 3(13, 12-14), 4(1), 5(2, 2-3), 6(1), 7(1, 1-2), 8(8, 8-12), 9(2, 1-3), 10(1), 11(4, 2-5), 12(1), 14(16, 11-19). Mesothorax: hair 1(5, 3-6), 2(1), 3(1), 4(1), 5(1), 6(5, 4-6), 7(1), 8(7, 6-8), 9(8, 6-9), 10(1), 11(2, 1-3), 12(1), 13(10, 6-16), 14(5, 5-9). Metathorax: hair 1(2, 1-4), 2(1), 3(4, 3-5), 4(7, 3-9), 5(9, 6-10), 6(1), 7(7, 6-9), 8(4, 3-5), 9(5, 4-7), 10(1), 11(2, 1-2), 12(1), 13(7, 4-7). *Abdomen*: Stellate hairs as on thorax. Segment I: hair 1(3, 2-3), 2(7, 6-8), 3(1), 4(4, 2-5), 5(7, 7-10), 6(3, 3-4), 7(1), 9(1, 1-2), 10(1), 11(7, 6-9), 13(5, 3-6). Segment II: hair 0(1), 1(2, 1-3), 2(7, 6-8), 3(1), 4(2, 2-4), 5(9, 7-10), 6(3), 7(3, 2-4), 8(1, 1-2), 9(6, 3-7), 10(1), 11(1), 12(1), 13(3, 3-5). Segment III: hair 0(1), 1(2, 2-3), 2(6, 5-8), 3(1), 4(2, 2-3), 5(10, 8-10), 6(1, 1-2), 7(5, 4-7), 8(1), 9(6, 5-6), 10(1), 11(1), 12(1), 13(5, 3-6), 14(1). Segment IV: hair 0(1), 1(2, 2-3), 2(7, 6-7), 3(1), 4(2, 2-3), 5(10, 8-11), 6(1, 1-2), 7(4, 4-8), 8(1, 1-2), 9(6, 5-7), 10(1), 11(1), 12(1), 13(5, 4-6), 14(1). Segment V: hair 0(1), 1(2), 2(6, 5-7), 3(1), 4(2, 2-5), 5(9, 7-10), 6(1), 7(3, 3-5), 8(1, 1-2), 9(6, 5-6), 10(1), 11(1), 12(1), 13(5, 4-7), 14(1). Segment VI: hair 0(1), 1(2), 2(5, 4-6), 3(1), 4(1), 5(6, 5-9), 6(1), 7(2, 2-3), 8(3, 1-3), 9(4, 4-6), 10(1), 11(1), 12(1), 13(7, 5-8), 14(1). Segment VII: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1), 5(3, 2-4), 6(3, 2-3), 7(1), 8(6, 4-7), 9(3, 2-3), 10(1), 11(1), 12(1), 13(3, 2-5), 14(1). *Segment VIII*: Comb scales in a single row, 18(16-19) in number; individual scale long and fringed uniformly to apex. Hair 0(1), 1(4, 3-5), 2(1), 3(6, 4-6), 4(1), 5(2, 2-3), 14(1). *Siphon*: Index about 6.0-6.5; moderately pigmented, with darker basal ring. Pecten extending to about 0.45, with 19(14-21) teeth; proximal teeth smooth, distal with a few apical spinules. Hair 1(2, 2-3), 2(1), 3-5 not visible, 6(1), 7(1), 8(2, 1-3), 9(1). *Anal Segment*: Saddle moderately pigmented; caudal margin with spines of varying sizes. Gills subequal, long, about 2.0 of saddle length. Hair 1(1), 2(5, 4-7), 3(1), 4a(4, 4-5), 4b(4), 4c(4, 3-5), 4d(4, 3-5), 4e(4, 3-4), 4f(3, 2-4).

SYSTEMATICS. *A. aurites* is undoubtedly a distinct species erroneously synony-

mized by Thompson (1956:199) with *inaequalis*. It is readily differentiated in the adult stage from all the other members of the group, as pointed out by Theobald (1907:217) in the original description, by the large continuous silvery patch on *ssp*. There are other diagnostic features in the adults as indicated above and the immature stages are readily separated from the other members of the group.

There is no striking variation in adult ornamentation in the small series of specimens examined and the diagnostic characters of the immature stages are quite constant.

BIONOMICS. The immature stages of *aurites* have been found only in arboreal bromeliads, in my experience generally at elevations of more than 3,500 feet and never in association with *grabhami* or *stenei*, the other bromeliad-breeding members of the Aurites Group. It appears that this species occurs at lower elevations at least occasionally as Thompson reared several adults from larvae collected at Hope Farm [USNM] at an elevation of 1,000 feet in 1946, and 2 females (JA 702) were caught recently (1967) near Kingston at elevations of about 1,000-1,500 feet. Females have been collected biting humans during the day but no attempt has been made to study their activity cycle. From the available data, *aurites* appears to have a restricted geographic range, having been collected only from the parishes of Manchester and St. Andrew.

DISTRIBUTION (fig.3). Endemic to the island of Jamaica where it has been reported from the parishes of Manchester, St. Andrew and Kingston, primarily at elevations of 3400 to 5250 ft. Material examined: 145 specimens; 24 ♂, 33 ♀, 44 pupae, 44 larvae; 36 individual rearings (22 pupal, 7 larval, 7 incomplete).

JAMAICA. *Manchester:* Hope Farm, 1 Jan 1946, G.A. Thompson, 2 lp♂ (460101-24,26), 1 l♂ (460101-30), 1 lp♀ (460101-27), 1 lp (460101-15); 1 Oct 1946, G.A. Thompson, 1 p (461001-1) [USNM]. *St. Andrew and Kingston:* Cinchona Gardens, elev. 4000-5250 ft, 8 Sept 1965, J.N. Belkin, 1 ♂ (JA 341); 24 Aug 1967, W.A. Page, 3 L (JA 752) [UCLA]. Ferry River, 4 Aug 1967, W.A. Page, 2 ♀ (JA 702) [UCLA]. Hardwar Gap, elev. 3800 ft, 1 lp♂ (647-20), 2 p♂ (647-110,111) [UCLA]. Kingston, July 1905, M. Grabham, 1 ♀ [USNM]. Newcastle, elev. 4000 ft, 5 Sept 1964, W.A. Page (JA 125), 1 lp♀ (125-10), 2 p♂ (125-102,106), 7 p♀ (125-100,101,103-105,107,114), 1 lP (125-11), 1 ♂, 7 ♀, 4 L; track to Catherines Peak, elev. 4000-4300 ft, 8 Nov 1966, O.G.W. Berlin, 2 p♂ (677-101,102), 1 p♀ (677-100), 5 ♀ (JA 679), 2 p♂ (680-110,111), 1 p♀ (680-112), 3 ♂, 1 P (JA 680), 1 lp♂ (681-10), 1 p♂ (681-100), 1 ♂, 2 ♀, 2 p, 7 L (JA 681), 1 p♂ (682-101), 3 p♀ (682-100,102,103), 3 lP (682-10-12), 3 ♂, 5 P, 13 L, 2 l (JA 682). Uester Road, elev. 3400-4500 ft, 8 Sept 1965, J.N. Belkin, 2 lP (337-12,13), 1 ♂, 1 ♀ (JA 337), 1 L (JA 338) [UCLA].

9. *Aedes* (Howardina) *grabhami* Berlin, n.sp.

Figs.3,7,8,21,22

TYPES: Holotype ♂ (JA 688-20) with associated pupal and larval skins and genitalia slide, near Hope Farm, Porus, Manchester, Jamaica, elev. 1000 ft, 12 Nov 1966, O.G.W. Berlin [USNM]. Allotype ♀ (JA 688-11) with associated pupal and larval skins, same data as holotype [USNM]. Paratypes: 11 ♂ (JA 688-13,100,101,107,108,111,114-116,126,128), 14 ♀ (JA 688-12,15,102,103,110,113,120-123,129-132), 1 lP (JA 688-16), 1 ♂, 5 p, 8 L, 1 l, same data as holotype [USNM, BM, UCLA].

1906.*Howardina aureostriata* Grabham, 1906:171-173. **TYPES:** ♂, ♀, larva, Newcastle (St. Andrew), Jamaica, elev. 4000 ft, Sept 1905, Loscombe and Maclaverty [NE].

Aedes (Howardina) *aureostriata* in part of Bonne and Bonne-Wepster (1925:370-371).
Aedes aureostriata of Gowdey (1926:73).

Aedes aureostriata in part of Howard, Dyar and Knab (1917:855-859); Dyar (1918:73,80).

Howardina aureostriata of Theobald (1910:609-611).

Haemagogus aureostriata of Dyar and Knab (1906a:166,167).

Aedes (Howardina) inaequalis in part of Thompson (1947:78; 1956:199-200); Stone, Knight and Starcke (1959:174); Belkin, Schick and Heinemann (1965:31); Forattini (1965:399,400).

Aedes inaequalis in part of Stone and Knight (1956:219).

Aedes (Howardina) aurites in part of Dyar (1928:236); Edwards (1932:155); Lane (1939:99; 1953:720-722); Horsfall (1955:471).

Aedes aurites in part of Hill and Hill (1948:29,42).

FEMALE. Wing: 2.15 mm. Proboscis: 1.68 mm. Forefemur: 1.33 mm. Abdomen: about 2.1 mm. Essentially similar to *aurites*, differing mainly in the following. *Head*: Erect scales entirely dark. *Thorax* (fig.8): Mesonotal dark scales not as dense as in *aurites*; light lines usually distinctly narrower than in *aurites*, in a few specimens broader than in *aurites* and rarely almost completely fused; outer dorsocentral line usually distinctly shorter, not merging with lateral marginal line anteriorly, in a few specimens merging with lateral marginal line; lateral marginal line long, moderately broad, extending from side of anterior promontory to wingbase. Antealar area above paratergite predominantly with scattered golden and a few bronzy scales. Lateral scutellar lobes with a few narrow golden scales only. *Apn* with a moderate silvery patch; *ssp* with a distinct silvery patch. Patches on base of *pra*, upper and lower *stp* distinct, separate. *Legs*: Midtarsus with few white scales on segments 1,2; hindtarsus with moderate white rings on 1-3. *Haltere*: Stem pale, knob predominantly white but with a few dark scales dorsally. *Abdomen*: Sternites II,III straw yellow, IV predominantly straw yellow, a few apical scales dark; rest of segments with basal yellow and distal dark scales.

MALE. Wing: 2.21 mm. Proboscis: 1.75 mm. Forefemur: 1.31 mm. Essentially similar to female in color.

MALE GENITALIA (fig.21). As figured; diagnostic characters as in the key. Ninth tergite lobe indistinct, with 2 strong bristles. Sidepiece length about 3.0 median width. Clasper length 0.65 of sidepiece, basal 0.33 with minute spicules; spiniform about 0.2 of clasper.

PUPA (fig.21). Abdomen: 2.75 mm. Trumpet: 0.38 mm; index 4.6-4.8. Paddle: 0.69 mm. Chaetotaxy as given below, hairs moderately pigmented. Readily separated from *inaequalis* and *stenei* by the absence of lightly pigmented area on metanotum and abdominal segments uniformly lightly pigmented; from *aurites* by the hair 2-VI distinctly mesad or at level of 3-VI. *Cephalothorax*: Mesonotum and metanotum lightly pigmented. Hair 1(1), 2(2, 2-3), 3(1), 4(7, 4-8), 5(5, 4-7), 6(1, 1-2), 7(4, 3-5), 8(1, 1-3), 9(1, 1-2), 10(22, 18-32), 11(1), 12(5, 3-6). *Abdomen*: Lightly pigmented, progressively lighter caudad. Segment I: hair 1(12-16 primary branches, subequal in length with many secondary branches), 2(2, 1-3), 3(1), 4(8, 6-8), 5(8, 4-8), 6(1, 1-2), 7(4, 3-4), 9(1), 10(1), 11(1). Segment II: hair 0(1), 1(60, 50-74), 2(1), 3(1), 4(5, 4-6), 5(1), 6(1), 7(5, 4-6), 9(1). Segment III: hair 0(1), 1(13, 8-17), 2(1), 3(1, 1-3), 4(4, 3-6), 5(1), 6(1), 7(4, 3-6), 8(4, 2-4), 9(1), 10(2, 2-3), 11(1), 14(1). Segment IV: hair 0(1), 1(9, 8-14), 2(1), 3(4, 4-6), 4(4, 2-4), 5(1), 6(1), 7(4, 3-6), 8(2, 1-4), 9(1), 10(2, 1-2), 11(1), 14(1). Segment V: hair 0(1), 1(1), 2(1), 3(2, 1-3), 4(4, 4-7), 5(1), 6(1), 7(5, 4-6), 8(2, 2-3), 9(1), 10(1, 1-2), 11(1), 14(1). Segment VI: hair 0(1), 1(1, 1-2), 2(1, 1-2), 3(2, 1-2), 4(4, 3-4), 5(1), 6(1), 7(1), 8(2, 2-3), 9(1), 10(1, 1-2), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(2, 1-2), 4(2), 5(1), 6(2, 2-5), 7(1), 8(3, 2-4), 9(2, 2-4), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(2, 1-2), 9(10, 8-11),

14(1). *Paddle*: Almost without pigmentation, midrib faintly pigmented. Male genital lobe extending to 0.42 of paddle, female genital lobe to 0.35.

LARVA (fig.22). Head: 0.7 mm. Siphon: 0.92 mm. Anal Saddle: 0.22 mm. Chaetotaxy as given below, hairs lightly to moderately pigmented. Readily separated from *stenei* by the small and single hair 2-VII; from *aurites* by hair 5-C always single; from *inaequalis* by hair 5-C single and longer, narrow gills. *Head*: Width about 1.14 of length. Mental plate with a strong median tooth and 10 distinct teeth (9-12) on each side, often a small detached tooth at base. Hair 0(1), 1(1), 3(1), 4(3, 2-5), 5(1), 6(6, 5-10), 7(3, 2-3), 8(1), 9(2, 2-3), 10(2, 1-2), 11(2, 1-7), 12(2, 2-4), 13(1), 14(1), 15(3, 2-4). *Antenna*: Length about 0.49 of head, very lightly pigmented and with a few scattered spicules. Hair 1-A at about 0.46 from base. *Thorax*: Stellate hairs with a few, weakly barbed branches; long hairs barbed, with attenuate apices. Prothorax: hair 0(7, 4-12), 1(6, 5-9), 2(1), 3(13, 8-19), 4(1, 1-2), 5(2, 1-2), 6(1), 7(1), 8(2, 2-11), 9(2, 1-2), 10(1), 11(2, 2-4), 12(1), 14(13, 9-22). Mesothorax: hair 1(2, 2-13), 2(1), 3(1), 4(1), 5(1), 6(4, 2-6), 7(1), 8(5, 4-7), 9(7, 6-8), 10(1), 11(2, 1-2), 12(1), 13(4, 2-4), 14(5, 4-7). Metathorax: hair 1(2, 1-12), 2(1), 3(4, 2-5), 4(2, 2-10), 5(5, 5-14), 6(1), 7(7, 6-8), 8(5, 4-8), 9(6, 6-9), 10(1), 11(2), 12(1), 13(4, 3-10). *Abdomen*: Long and stellate hairs as on thorax. Segment I: hair 1(3, 2-14), 2(6, 6-14), 3(1), 4(4, 3-4), 5(4, 4-12), 6(3), 7(1), 9(1), 10(1), 11(5, 5-11), 13(4, 4-11). Segment II: hair 0(1), 1(2, 2-12), 2(5, 5-13), 3(1), 4(2, 2-4), 5(7, 5-14), 6(3, 2-3), 7(2, 2-3), 8(1), 9(5, 5-9), 10(1), 11(1), 12(1), 13(3, 2-8). Segment III: hair 0(1), 1(2, 2-3), 2(5, 5-11), 3(1), 4(2, 2-3), 5(7, 5-12), 6(1, 1-2), 7(6, 3-7), 8(1), 9(5, 4-9), 10(1), 11(1), 12(1), 13(2, 2-8), 14(1). Segment IV: hair 0(1), 1(2, 1-3), 2(5, 5-12), 3(1), 4(2, 2-3), 5(6, 6-14), 6(1), 7(6, 5-7), 8(1), 9(5, 5-9), 10(1), 11(1), 12(1), 13(3, 3-8), 14(1). Segment V: hair 0(1), 1(2, 2-3), 2(5, 5-10), 3(1), 4(4, 3-5), 5(5, 4-13), 6(1), 7(6, 3-7), 8(1), 9(5, 5-7), 10(1), 11(1), 12(1), 13(3, 2-8), 14(1). Segment VI: hair 0(1), 1(2, 1-3), 2(4, 4-8), 3(1), 4(1), 5(2, 2-9), 6(1), 7(3, 2-5), 8(3, 2-3), 9(3, 2-7), 10(1), 11(1), 12(1), 13(3, 2-11), 14(1). Segment VII: hair 0(1), 1(2, 1-2), 2(1), 3(1), 4(1), 5(3, 2-3), 6(3, 2-5), 7(1), 8(5, 5-10), 9(1, 1-2), 10(1), 11(1), 12(1), 13(1, 1-3), 14(1). *Segment VIII*: Comb scales 16(15-19), moderately pigmented, elongate, fringed on sides and apex. Hair 0(1), 1(3, 3-4), 2(1), 3(5, 4-7), 4(1), 5(2, 2-5), 14(1). *Siphon*: Index about 6.8-8.5; moderately pigmented, with darker basal ring. Pecten extending to about 0.44; teeth 17(14-22). Hair 1(2, 2-3), 2(1), 3-5 not visible, 6(1), 7(1), 8(2, 1-2), 9(1). *Anal Segment*: Saddle moderately pigmented. Gills narrow, length about 1.5 of saddle, ventral 0.8 of dorsal. Hair 1(1), 2(5, 5-8), 3(1), 4a(5, 4-7), 4b(5, 4-5), 4c(4, 3-5), 4d(4, 4-5), 4e(4, 2-6), 4f(3, 2-4).

SYSTEMATICS. Although it is almost certain that *grabhami* represents the same taxon as *aureostriatus* Grabham, 1907, which is preoccupied in *Aedes* by *aureostriatus* (Doleschall, 1857) and *aureostriatus* (Leicester, 1908), I am proposing it as a new species and not as a replacement name for *aureostriatus* because the types of the latter are lost and therefore the identity of this nominal taxon cannot be objectively determined. This species was believed to be identical with *inaequalis* and *aurites* by Thompson (1956) who used the former name because of priority. *A. grabhami* is readily differentiated from the other species of the *Aurites* Group in all stages by the characters indicated in the diagnosis and keys.

There is considerable variation in the ornamentation of adults of *grabhami*. The majority have distinct golden mesonotal lines, broader than in *inaequalis* and *stenei* and narrower than in *aurites*; a few have these lines narrower than in *inaequalis* or *stenei*. The most striking departure is found in a few specimens with the mesonotum almost completely golden except for a few dark scales in indistinct narrow longitu-

dinal lines; in these the hindtarsal light markings are restricted to segments 1 and 2. I have retained these specimens under *grabhami* on the basis of similarity in other diagnostic features but their exact taxonomic status is doubtful. They may represent a distinct species or possibly hybrids between typical *grabhami* and *stenei* which have been found in the same collections. There is also considerable variation in the chaetotaxy of the larvae, some being much more "hairy" than others; however, the diagnostic characters given above apply to all the material I have seen.

BIONOMICS. The immature stages of *grabhami* are found in both terrestrial and epiphytic bromeliads. *A. stenei* is frequently associated with *grabhami* in the same bromeliads but it is not known if the 2 species actually occupy the same axils. I did not find *grabhami* above 1,800 feet elevation but the original material of *aureostriatus* is reported to have been collected at an altitude of about 4,000 feet. *A. grabhami* is, next to *stenei*, the most common member of the Aurites Group and has been reported from all parishes of Jamaica except Westmoreland, Trelawny and St. Elizabeth. Females were found to bite humans along with *stenei* and *inaequalis* and showed the same small peak of biting activity at 1700 hrs, as the latter (fig.7).

DISTRIBUTION (fig.3). Endemic to the island of Jamaica where it has been reported from all parishes except Westmoreland, Trelawny and St. Elizabeth at elevations of 100 ft to 1800 ft. Material examined: 1223 specimens; 172 ♂, 385 ♀, 373 pupae, 293 larvae; 298 individual rearings (198 pupal, 69 larval, 31 incomplete).

JAMAICA. *Clarendon*: Belcarres, 7 Nov 1967, W.A. Page (JA 902), 1 p♂ (902-101), 1 p♀ (902-102), 3 L [UCLA]. *Hanover*: Lethe, elev. 500 ft, 6 Nov 1966, O.G.W. Berlin and D.C. Watson, 2 L (JA 667) [UCLA]. *Manchester*: Hope Farm, 8 July 1945, G.A. Thompson, 1 lp♂ (450708-2), 2 lp♀ (450708-9,11), 1 lp (450708-7), 1 l (450708-8); 1 Aug 1945, G.A. Thompson, 1 l♂ (450801-12), 1 ♀ (450801-12), 2 l (450801-6,8); 1 Oct 1945, G.A. Thompson, 2 lp♂ (451001-6,9), 1 l♂ (451001-1), 1 lp (451001-14); Oct 1945, 3 L; 1 Jan 1946, G.A. Thompson, 2 lp♀ (460101-4,12), 1 ♂ (460101-15); 8 Jan 1946, 1 ♂, 1 ♀ [USNM]; elev. 1000-1100 ft, 10 Sept 1965, W.A. Page, 1 lp♀ (354-12), 2 p♂ (354-105,106), 3 p♀ (354-103,104,107), 1 ♂ (JA 355), 1 ♀ (JA 356); 12 Nov 1966, O.G.W. Berlin, 210 ♀ (JA 684), 2 p♂ (686-100,102), 1 p♀ (686-101), 2 lp♀ (687-11,12), 5 p♂ (687-100-104), 1 IP (687-10), 1 P (JA 687), 2 lp♂ (688-13,20), 3 lp♀ (688-11,12,15), 10 p♂ (688-100,101,107,108,111,114-116,126,128), 12 p♀ (102,103,110,113,120-123,129,130-132), 1 IP (688-16), 1 ♂, 5 p, 8 L, 1 l (JA 688, type series) [UCLA]. *Mandeville*, 5 Mar 1928, Pickering, 5 ♀ [USNM]. *Porus*, elev. 900-1000 ft, 23 Oct 1966, O.G.W. Berlin and D.C. Watson, 1 lp♂ (630-11), 1 lp♀ (630-10), 1 L (JA 630), 4 p♂ (631-105,106,109,112), 2 p♀ (631-108,113), 2 ♀, 1 P, 2 p, 1 L, 1 l (JA 631), 2 lp♂ (632-10,12), 1 lp♀ (632-11), 6 p♂ (632-101,103,104,108,112,114), 5 p♀ (632-100,102,105-107), 2 IP (632-13,15), 1 P, 2 p, 19 L, 2 l (JA 632); 1 Nov 1966, O.G.W. Berlin, 1 lp♂ (655-10), 6 p♂ (655-101,103,105-107,109), 4 p♀ (655-100,104,108,111), 4 IP (655-11-14), 4 L, 6 l (JA 655), 2 L (JA 656), 2 p♂ (658-110,114), 4 p♀ (658-103,107,112,113), 1 ♂, 1 p, 1 L, 1 l (JA 658) [UCLA]. *Portland*: Kemney-Sherwood Forest, elev. 750 ft, 12 Aug 1967, J.N. Belkin and W.A. Page, 1 lp♂ (706-11), 1 p♀ (706-100), 1 p (JA 706), 2 lp♀ (708-13,16), 1 p♂ (708-11), 1 lp (708-14), 1 ♀ (JA 708) [UCLA]. *St. Andrew and Kingston*: Hermitage Dam Road, 1 Sept 1965, W.A. Page (JA 319), 1 lp♀ (319-105); 17 Aug 1967, J.N. Belkin and W.A. Page, 2 lp♂ (723-21,23), 1 lp♀ (723-24), 1 IP (723-20), 2 p♀ (725-113A,114), 1 ♂, 1 P (JA 725); 5 July 1967, W.A. Page and J.N. Belkin (JA 765), 1 p♂ (765-100); 25 Aug 1967, W.A. Page (JA 854), 1 lp♂ (854-13), 2 p♂ (854-105,106), 1 p♀ (854-107), 2 IP (854-15,16), 2 L; 5 Aug 1967, W.A. Page and J.N. Belkin (JA 892), 4 lp♂ (892-10,13,15,16), 3 lp♀ (892-11,12,14), 2 p♂ (892-100,104), 3 P, 1 L [UCLA]. *Kingston*, M. Grabham, 1 ♂ [USNM]. *St. Ann*: Moneague, 17 Aug 1967, J.N. Belkin and W.A. Page (JA 733), 1 p♂ (733-105), 4 p♀ (733-40,90,96,114), 2 ♂, 1 P, 6 p, 3 L, 1 l [UCLA]; Faiths Pen Schoolyard, elev. 1750 ft, 31 Aug 1967, W.A. Page (JA 762), 2 p♂ (762-100,101), 1 ♂, 1 ♀, 1 P, 1 l [UCLA]; 2.0 mi S of Moneague near Unity, elev. 1750 ft, 25 Aug 1967, W.A. Page (JA 758), 6 p♂ (758-100,103,104,109,110,113), 2 p♀ (758-30,101), 1 ♂, 2 ♀, 3 p [UCLA]; 29.0 mi S of Moneague, elev. 1750 ft, 30 Aug 1967, W.A. Page, 1 ♂, 2 ♀, 4 P, 3 l (JA 763), 2 lp♂ (764-10,12), 1 lp♀ (764-30),

9 p♂ (764-91,94,95,99 103-106,109), 5 p♀ (764-92,98,100,102,108), 2 ♂, 1 ♀, 8 P, 6 p, 21 L (JA 764) [UCLA]; Moneague-Clairemont Road, 17 Sept 1965, W.A. Page, 1 lp♂ (375-12), 1 lp♀ (375-13), 1 p♀ (375-100), 7 ♀ (JA 375), 1 p♂ (378-100), 1 p♀ (378-101), 1 IP (378-13), 1 lp♂ (380-12), 4 lp♀ (380-10,11,13,17A), 3 p♂ (380-101,104,105), 2 p♀ (380-100,107), 5 IP (380-14,15,17,18, 20) [UCLA]; Moneague-Ocho Rios Road, 10 Sept 1967, W.A. Page (JA 776), 1 p♀ (776-101) [UCLA]. Mt. Diablo, 17 Sept 1965, W.A. Page (JA 376), 1 lp♀ (376-12); 17 Aug 1967, J.N. Belkin and W.A. Page, 6 lp♂ (731-21,33,35-38), 1 lp♀ (731-31), 9 p♂ (731-90,92,93,105,108-112), 12 p♀ (731-80,81,91,94,97,99,103-107,113), 2 IP (731-30,34), 11 ♂, 7 ♀, 2 P, 17 p, 24 L (JA 731), 1 lp♂ (732-10), 10 p♂ (732-70,94,97,100-102,104,111,112,114), 6 p♀ (732-90,92,93,105,107,108), 1 ♀, 1 P, 3 p, 5 L, 2 I (JA 732), 4 lp♂ (733-13-16), 1 p♂ (733-100), 1 IP (733-11), 12 L (JA 733), 1 p♂ (734-102), 2 p♀ (734-101,105), 2 P, 1 L (JA 734), 1 ♀ (JA 735) [UCLA]. *St. Elizabeth*: Darlington, 28 Oct 1967, W.A. Page, 1 p, 4 L (JA 901) [UCLA]. *St. James*: Five Miles, elev. 100 ft, 6 Nov 1966, O.G.W. Berlin and D.C. Watson (JA 676), 1 lp♀ (676-11), 2 p♂ (676-115,121), 6 p♀ (676-104,107,112,113,116,123), 1 IP (676-17), 1 ♂, 1 ♀, 3 p, 2 L [UCLA]. Montego Bay, elev. 500 ft, 6 Nov 1966, O.G.W. Berlin and D.C. Watson (JA 669), 1 IP (669-11) [UCLA]. Reading, elev. 200 ft, 6 Nov 1966, O.G.W. Berlin and D.C. Watson, 1 I (JA 670) [UCLA]. *St. Mary*: Broadgate, elev. 500 ft, 27 Oct 1966, O.G.W. Berlin and D.C. Watson (JA 643), 2 lp♂ (643-33,43), 1 lp♀ (643-37), 1 L, 1 I [UCLA]. Leith Hall, 13 Nov 1966, O.G.W. Berlin and D.C. Watson, 4 L (JA 689) [UCLA]. Windsor Forest, elev. 750 ft, 30 Oct 1966, O.G.W. Berlin and D.C. Watson, 1 lp♀ (650-22), 4 p♂ (650-100-102,105), 2 IP (650-20,23), 1 ♂, 6 P, 3 L (JA 650), 1 IP (651-34), 2 lp♀ (652-10,12), 4 p♂ (652-100,102,103,110), 4 p♀ (652-101,104,108,111), 2 IP (652-14,15), 11 L, 1 I (JA 652) [UCLA]. *Parish not specified*: 1944, R.B. Hill, 1 ♂; 1 Jan 1946, G.A. Thompson, 7 L; M. Grabham, 1 lp; G.A. Thompson, 1 ♂, 2 ♀ [USNM]; W.A. Page, 2 p♂ (771-101,106), 4 L (JA 771), 2 lp♀ (772-33, 34), 8 p♂ (772-90,93,95,97,99,106,110,114), 11 p♀ (772-91,92,96,98,101,103,104,107,108,111, 113), 1 lp (772-30), 3 ♂, 6 ♀, 5 P, 11 p, 40 L, 1 I (JA 772) [UCLA].

10. *Aedes (Howardina) inaequalis* (Grabham)

Figs. 3, 7, 8, 23, 24

1907. *Howardina inaequalis* Grabham, 1907:25-26. TYPE: Lectotype ♂ with genitalia slide, Kingston (St. Andrew), Jamaica, date not specified, M. Grabham [USNM; selection of Stone and Knight 1956:219].

Aedes (Howardina) inaequalis in part of Thompson (1947:78; 1956:199-200); Stone, Knight and Starcke (1959:174); Belkin, Schick and Heinemann (1965:31); Forattini (1965:399,400); Porter (1967:38).

Aedes inaequalis in part of Stone and Knight (1956:219).

Howardina inaequalis of Theobald (1910:611); Surcouf and Gonzalez-Rincones (1911:141).

Aedes (Howardina) aurites in part of Dyar (1928:236); Edwards (1932:155); Lane (1939:99; 1953:720-722); Horsfall (1955:471).

Aedes aurites in part of Hill and Hill (1948:29,42).

Aedes (Howardina) aureostriata in part of Bonne and Bonne-Wepster (1925:370-371).

Aedes aureostriata in part of Howard, Dyar and Knab (1917:855-859); Dyar (1918:73,80).

FEMALE. Wing: 2.37 mm. Proboscis: 1.93 mm. Forefemur: 1.49 mm. Abdomen: about 2.1 mm. Similar to *aurites*, differing primarily in the following. *Head*: Erect scales dark. *Thorax* (fig.8): Mesonotal dark scales not dense as in *aurites*; mesonotal light lines narrow, faintly golden, distinctly narrower than dark lines; outer dorsocentral line shorter, not merging with lateral marginal line anteriorly. Lateral marginal line narrow from side of anterior promontory to wingbase. Antealar area above paratergite with scattered dark scales only. Lateral scutellar lobes with a few narrow golden scales. *Apn* with a restricted silvery patch, distinctly smaller than in *aurites* and

grabhami; *ssp* with a distinct silvery patch; patches on base of *pra*, upper and lower *stp* distinct, separate. *Legs*: Midtarsus with a few white scales on segments 1,2; hind-tarsus with broader white rings on 1-3. *Haltere*: Stem pale, knob predominantly white, with a few dark scales dorsally. *Abdomen*: Basomedian tergal straw yellow patches on V-VII.

MALE. Wing: 2.36 mm. Proboscis: 2.01 mm. Forefemur: 1.58 mm. Essentially similar to female in coloration.

MALE GENITALIA (fig.23). Diagnostic characters as in the key. Ninth tergite lobe not prominent, with 2,3 bristles. Sidepiece length about 2.5 median width. Clasper length about 0.55 of sidepiece; spiniform short, about 0.25 of clasper.

PUPA (fig.23). Abdomen: 3.08 mm. Trumpet: 0.46 mm; index 5.0-5.6. Paddle: 0.68 mm. Chaetotaxy as given below, hairs lightly to moderately pigmented. Very similar to *stenei* but apparently distinguishable by the moderately pigmented abdominal tergite II and segment III only slightly darkened in the middle, without distinct dark stripe. Readily separated from *aurites* and *grabhami* by the lightly pigmented area on the metanotum. *Cephalothorax*: Mesonotum moderately pigmented between trumpets; lateral area slightly darker; metanotum with a small to moderate, lightly pigmented area in the middle of lateral portion. Hair 1(1), 2(2, 1-3), 3(1, 1-3), 4(4, 2-7), 5(6, 3-7), 6(1, 1-2), 7(4, 3-6), 8(1, 1-2), 9(2, 2-3), 10(15, 6-15), 11(1), 12(4, 2-5). *Abdomen*: Tergite I moderately pigmented except for usual membranous areas; tergites II,III moderately pigmented; other segments lighter. Segment I: hair 1(11-14 primary branches, subequal in length, each with many secondary branches), 2(1, 1-2), 3(1), 4(5, 4-7), 5(5, 4-6), 6(1), 7(3, 2-3), 9(1), 10(1, present in some), 11(1, present in some). Segment II: hair 0(1), 1(40, 36-56), 2(1), 3(1), 4(4, 4-8), 5(1), 6(1), 7(4, 3-4), 9(1), 10(2, 2-3, present in a few). Segment III: hair 0(1), 1(9, 9-20), 2(1), 3(1), 4(4, 2-4), 5(1), 6(1), 7(4, 2-5), 8(3, 2-3), 9(1), 10(2), 11(1), 14(1). Segment IV: hair 0(1), 1(6, 3-14), 2(1), 3(4, 3-7), 4(2, 2-3), 5(1, 1-2), 6(1), 7(3, 2-4), 8(2, 1-2), 9(1), 10(2, 1-2), 11(1), 14(1). Segment V: hair 0(1), 1(1, 1-4), 2(1), 3(2, 1-3), 4(6, 3-7), 5(1, 1-2), 6(1), 7(5, 3-7), 8(2, 1-3), 9(1), 10(1, 1-2), 11(1), 14(1). Segment VI: hair 0(1), 1(1, 1-3), 2(1), 3(1, 1-3), 4(3, 2-7), 5(1, 1-2), 6(1, 1-2), 7(1, 1-2), 8(3, 2-4), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1), 4(2, 1-3), 5(1), 6(3, 2-4), 7(1, 1-3), 8(3, 1-5), 9(4, 3-5), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(2, 1-2), 9(9, 8-12), 14(1, 1-2). *Paddle*: Uniformly lightly pigmented, midrib slightly darker; external margin smooth; hair 1-P slender. Male genital lobe extending to 0.56 of paddle, female genital lobe to 0.36.

LARVA (fig.24). Head: 0.7 mm. Siphon: 0.9 mm. Anal Saddle: 0.22 mm. Readily separated from other species by the short, broad unequal gills and hair 5-C usually double. *Head*: Width about 1.12 of length. Mental plate with a strong median tooth and 11 distinct teeth (11-12) on either side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(3, 2-4), 5(2, 1-2), 6(9, 8-11), 7(4, 3-4), 8(1), 9(2, 2-3), 10(1), 11(2, 2-5), 12(1, 1-2), 13(1), 14(1), 15(3, 2-3). *Antenna*: Length about 0.46 of head; pigmentation very light; shaft with very few minute scattered spicules. Hair 1-A about 0.5 from base. *Thorax*: Stellate hairs with a few unequal branches; long hairs barbed and with attenuate apices. Prothorax: hair 0(4, 2-8), 1(3, 3-7), 2(1), 3(5, 4-6), 4(1, 1-2), 5(2), 6(1), 7(1, 1-2), 8(3, 2-4), 9(1, 1-2), 10(1), 11(2, 2-4), 12(1), 14(10, 9-12). Mesothorax: hair 1(2, 2-5), 2(1), 3(1), 4(1), 5(1), 6(4, 4-5), 7(1), 8(6, 5-8), 9(7, 5-8), 10(1), 11(2, 2-3), 12(1), 13(11, 7-11), 14(5, 4-5). Metathorax: hair 1(2, 2-4), 2(1), 3(4, 3-5), 4(2, 2-4), 5(5, 4-6), 6(1), 7(6, 5-7), 8(5, 5-9), 9(5, 5-7), 10(1), 11(2, 1-2), 12(1), 13(4, 1-5). *Abdomen*: Long and stellate hairs as on thorax. Segment I: hair 1(3, 2-7), 2(5), 3(1), 4(3, 3-4), 5(4, 3-6), 6(3, 2-3), 7(1, 1-2), 9(1),

10(1), 11(6, 5-8), 13(3, 2-7). Segment II: hair 0(1), 1(2, 2-6), 2(5, 4-6), 3(1), 4(2, 2-4), 5(6, 4-8), 6(3, 2-3), 7(3, 2-4), 8(1, 1-2), 9(5, 4-6), 10(1), 11(1), 12(1), 13(2, 2-4). Segment III: hair 0(1), 1(2, 2-4), 2(5, 5-6), 3(1), 4(2), 5(5, 5-8), 6(1), 7(5, 3-6), 8(1), 9(5, 4-5), 10(1), 11(1), 12(1), 13(4, 2-8), 14(1). Segment IV: hair 0(1), 1(2, 2-4), 2(6, 5-6), 3(1), 4(2), 5(7, 5-9), 6(1), 7(5, 3-6), 8(1), 9(5, 4-5), 10(1), 11(1), 12(1), 13(5, 3-10), 14(1). Segment V: hair 0(1), 1(3, 2-4), 2(5, 5-6), 3(1), 4(2, 1-3), 5(6, 5-9), 6(1), 7(5, 3-5), 8(1, 1-2), 9(5, 4-6), 10(1), 11(1), 12(1), 13(4, 2-9), 14(1). Segment VI: hair 0(1), 1(2, 2-3), 2(4, 4-5), 3(1), 4(1), 5(4, 2-6), 6(1), 7(3, 2-4), 8(3, 1-3), 9(3, 2-4), 10(1), 11(1), 12(1), 13(3, 2-4), 14(1). Segment VII: hair 0(1), 1(2), 2(1), 3(1), 4(1), 5(2, 2-3), 6(4, 2-5), 7(1), 8(7, 6-9), 9(3, 2-4), 10(1), 11(1), 12(1), 13(2), 14(1). *Segment VIII*: Comb scales 16(14-18) in number; individual scale moderately pigmented, elongate, fringed on sides and apex. Hair 0(1), 1(4, 3-5), 2(1), 3(5, 5-6), 4(1), 5(3, 3-5), 14(1). *Siphon*: Index about 4.25 to 5.3; moderately pigmented but with darker basal ring. Pecten extending to about 0.4, 19(16-25) teeth; individual tooth narrow, long, with minute spinules in distal half. Hair 1(2), 2(1), 3-5 not visible, 6(1), 7(1), 8(1), 9(1). *Anal Segment*: Saddle moderately pigmented. Gills as long as or slightly shorter than saddle length, broad, unequal, ventral 0.64 of dorsal. Hair 1(1), 2(5, 4-5), 3(1), 4a(4, 3-4), 4b(4), 4c(4, 3-4), 4d(4), 4e(3), 4f(3, 1-3).

SYSTEMATICS. Contrary to the opinion of Thompson (1956:199), *inaequalis* is a species distinct from *aureostriatus* (now *grabhami*) and *aurites*. The adults of these 3 forms are readily distinguished from one another by the characters mentioned in the diagnoses and keys but I have not been able to find any reliable characters to separate *inaequalis* from Thompson's *stenei* which, however, I consider to be also a distinct species. The larva of *inaequalis* is clearly differentiated from the other members of the group but the pupa is very similar to that of *stenei*. Furthermore, an ecological barrier separates *inaequalis* from the rest of the group as this species is never found breeding in bromeliads to which the other species are confined. *A. inaequalis* is found primarily at low elevations and seldom above 1,500 feet. I have seen specimens of *inaequalis* only from the parishes of Clarendon, Kingston, Manchester, Portland, St. Andrew, St. Catherine, St. Mary and St. Thomas. This species may be more widely distributed and more common than the records indicate because these are based on immature stages only and these breeding sites have not been as widely sampled as those of the other species of the group.

BIONOMICS. *A. inaequalis* has been found breeding primarily in treeholes and cut and broken bamboo but has also been taken occasionally in rockholes and crabholes. There are no records of this species breeding in bromeliads. Since adults cannot be distinguished at present from *stenei*, it is not known if females of *inaequalis* bite humans but it is possible that some females of this species are included in the *stenei-inaequalis* material obtained in the 24-hour biting-landing survey (fig.7).

DISTRIBUTION (fig.3). Endemic to the island of Jamaica where it has been reported from the parishes of Clarendon, Kingston, Manchester, Portland, St. Andrew, St. Catherine, St. Mary and St. Thomas from near sea level to about 1000 ft. Material examined: 574 specimens; 55 ♂, 81 ♀, 99 pupae, 339 larvae; 83 individual rearings (47 pupal, 28 larval, 8 incomplete).

JAMAICA. *Clarendon*: May Pen, 10 Sept 1965, rockholes, J.N. Belkin (JA 352), 6 p♂ (352-100A, 102, 104, 106, 107, 109), 6 p♀ (352-32, 90, 91, 93, 108, 111), 1 IP (352-12), 6 ♂, 8 ♀, 1 P, 8 p, 37 L; 6 Sept 1966, rockholes, D.C. Watson (JA 602), 1 p♂ (602-101), 1 p♀ (602-100), 5 ♂, 7 ♀; 1 Sept 1966, rockholes, D.C. Watson, 2 ♂ (JA 603) [UCLA]. *Manchester*: Hope Farm, elev. 900-1000 ft, 23 Oct 1966, treehole, O.G.W. Berlin and D.C. Watson (JA 634), 2 lp♂ (634-10, 17), 5 lp♀ (634-11-13, 15, 19), 2 p♂ (634-102, 104), 3 p♀ (634-100-102), 4 IP (634-14, 16, 18, 20), 1 L, 1 l

[UCLA]. *Portland*: Kemney-Sherwood Forest, elev. 750 ft, 13 Aug 1967, bamboo, J.N. Belkin and W.A. Page, 1 lp♂ (713-10), 1 p♂ (713-100), 16 L (JA 713), 2 lp♂ (715-10,11), 2 p♂ (715-100, 102) [UCLA]. *St. Andrew and Kingston*: Constant Springs, 16 Nov 1966, treehole, O.G.W. Berlin and D.C. Watson, 6 L (JA 696) [UCLA]. *Ferry Quarry*, 13 Sept 1965, crabhole, W.A. Page, 1 ♀ (JA 369) [UCLA]. *Hermitage Dam Road*, 20 Aug 1964, rockhole, L. Paton (JA 109), 2 lp♂ (109-10,11), 1 p♂ (109-101), 1 p♀ (109-100), 4 ♂, 1 ♀, 1 P, 2 L; 22 Aug 1965, treehole, W.A. Page (JA 280), 1 p♂ (280-102), 1 ♂; 10 Aug 1965, treehole, W.A. Page (JA 288), 2 lp♀ (288-10,15), 1 p♂ (288-102), 1 ♂; 13 Aug 1965, bamboo, W.A. Page, 1 lp♂ (290-14), 3 lp♀ (290-10,11,13), 2 L (JA 292), 25 L (JA 293), 6 L (JA 294), 1 lp♀ (295-23), 2 ♂, 1 ♀, 10 L (JA 296), 1 L (JA 298), 1 ♀ (JA 299), 1 p♀ (300-20), 2 L (JA 300), 17 L (JA 302), 1 lp♀ (304-22), 3 L (JA 307), 24 L (JA 308), 1 ♂, 1 ♀, 1 P (JA 309); 7 Sept 1965, J.N. Belkin, 1 ♀, 2 L (JA 330), 3 L (JA 331); 29 Oct 1965, treehole, W.A. Page, 1 p♂ (390-100A), 2 p♀ (390-101,102), 1 p♀ (397-105); 13 July 1967, treehole, W.A. Page (JA 826), 1 p♀ (826-20) [UCLA]. *Mt. Salus*, 17 Sept 1967, bamboo, W.A. Page, 123 L (JA 780) [UCLA]. *Temple Hall*, elev. 500 ft, 20 Aug 1965, bamboo, W.A. Page, 1 p♀ (250-102), 1 ♂, 1 ♀, 1 P, 5 L (JA 250), 1 lp♂ (252-35), 4 lp♀ (252-102,105,107,108), 1 ♂, 1 p, 6 L, 1 l (JA 252); 25 Aug 1965, bamboo, D.C. Watson (JA 251), 1 p♂ (251-107), 1 lP (251-60), 1 ♂, 11 L [UCLA]. *Waterworks*, 7 Sept 1965, treehole, J.N. Belkin (JA 327), 1 p♀ (327-104), 1 ♀, 1 p, 1 L; 3 Dec 1965, treehole, W.A. Page (JA 408), 1 lP (408-14) [UCLA]. *St. Catherine*: Harkers Hall, elev. 750 ft, 12 July 1967, bamboo, W.A. Page (JA 822), 2 lp♀ (822-12,14), 1 lP (822-10), 1 ♂, 1 p, 5 L [UCLA]. *Rio Cobre Dam*, elev. 100 ft, 10 Sept 1965, treehole, J.N. Belkin (JA 351), 1 lp♀ (351-30), 1 p♀ (351-105), 1 lP (351-31), 1 L; 17 Sept 1965, ditch, D.C. Watson, 1 ♂ (JA 372), treehole, 1 ♂, 3 ♀, 1 p (JA 373) [UCLA]. *Spanish Town*, 9 Sept 1965, treehole, D.C. Watson (JA 605), 1 p♂ (605-102) [UCLA]. *St. Mary*: Prospect, 3 Nov 1964, rockhole, W.A. Page, 1 ♂, 1 ♀, 1 p (JA 173) [UCLA]. *St. Thomas*: Folly, elev. 50 ft, rockhole (JA 103), 4 p♀ (103-102,103,105,108), 1 ♀ [UCLA]. *Parish not specified*: Jan 1940, bamboo, 1 ♂, 2 ♀ [USNM].

11. *Aedes (Howardina) stenei* Thompson

Figs. 3, 7, 8, 25, 26

1956. *Aedes stenei* Thompson, 1956:196-199. TYPE: Holotype ♂ (45090211) with associated larval skin and male genitalia slide, near Hope Farm, just above Porus, on road to Mandeville, Manchester (as Clarendon), Jamaica, elev. about 1000 ft, Sept 1945, G.A. Thompson [USNM].

Aedes (Howardina) stenei of Stone, Knight and Starcke (1959:174); Belkin, Schick and Heine-mann (1965:31); Forattini (1965:471); Porter (1967:38).

FEMALE. Wing: 2.57 mm. Proboscis: 1.66 mm. Forefemur: 1.58 mm. Abdomen: about 2.02 mm. Essentially similar to *inaequalis* from which it cannot be separated (fig. 8).

MALE. Wing: 2.38 mm. Proboscis: 2.1 mm. Forefemur: 1.58 mm. Essentially similar to female in coloration.

MALE GENITALIA (fig. 25). Diagnostic characters as in the key. Ninth tergite lobe indistinct, with 2, 3 strong bristles. Sidepiece length about 2.5 median width. Clasper about 0.6 of sidepiece length, basal 0.33 with small spicules; spiniform about 0.25 of clasper.

PUPA (fig. 25). Abdomen: 2.24 mm. Trumpet: 0.38 mm; index about 5.0. Paddle: 0.68 mm. Chaetotaxy as given below, hairs lightly to moderately pigmented. Very similar to *inaequalis* but distinguished by the deeply pigmented abdominal tergite II and by the presence of a distinct narrow median longitudinal dark stripe on tergite III. Readily separated from *aurites* and *grabhami* by the 2-branched hair 9-C and the lightly pigmented area on the metanotum. *Cephalothorax*: Mesonotum moderately

pigmented between trumpets, lateral areas slightly darker; metanotum with a lightly pigmented area in the middle of lateral portion. Hair 1(1), 2(2, 2-3), 3(1), 4(5, 4-7), 5(5, 4-9), 6(1, 1-2), 7(4, 3-9), 8(1, 1-2), 9(2, 2-3), 10(10, 7-18), 11(1), 12(5, 3-7). *Abdomen*: Tergite I moderately pigmented except for usual membranous areas; tergite II strongly pigmented; tergite III with distinct narrow, median, dark longitudinal stripe; pigmentation progressively lighter caudad. Segment I: hair 1(12-17 primary branches, subequal in length each with several secondary branches), 2(1, 1-2), 3(1), 4(6, 4-8), 5(4, 3-8), 6(1), 7(3, 1-3), 9(1), 10(1), 11(1). Segment II: hair 0(1), 1(46, 36-72), 2(1), 3(1), 4(5, 3-6), 5(1), 6(1), 7(4, 2-5), 9(1), 10(1, 1-4, present in some). Segment III: hair 0(1), 1(16, 7-23), 2(1), 3(1, 1-2), 4(3, 2-4), 5(1, 1-2), 6(1), 7(3, 2-4), 8(2, 2-4), 9(1), 10(2, 1-2), 11(1), 14(1). Segment IV: hair 0(1), 1(10, 4-19), 2(1), 3(5, 3-6), 4(3, 1-4), 5(1, 1-3), 6(1), 7(2, 2-4), 8(2, 1-3), 9(1), 10(2, 1-2), 11(1), 14(1). Segment V: hair 0(1), 1(2, 1-7), 2(1), 3(2, 1-3), 4(4, 3-6), 5(1, 1-2), 6(1), 7(4, 2-5), 8(2, 1-3), 9(1), 10(1, 1-2), 11(1), 14(1). Segment VI: hair 0(1), 1(2, 1-4), 2(1), 3(2, 1-2), 4(3, 2-5), 5(1, 1-4), 6(1, 1-2), 7(1), 8(2, 2-4), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1, 1-2), 4(2, 1-2), 5(1), 6(3, 2-4), 7(1), 8(4, 3-5), 9(5, 3-6), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(2, 1-2), 9(10, 8-13), 14(1). *Paddle*: Uniformly very lightly pigmented, midrib slightly darker; external margin smooth. Male genital lobe extending to 0.42 of paddle, female genital lobe to 0.38.

LARVA (fig.26). Head: 0.7 mm. Siphon: 0.95 mm. Anal Saddle: 0.27 mm. Readily separated from other members of the group by the strong, 4-7-branched hair 2-VII. *Head*: Width about 1.02 of length. Mental plate with a strong median tooth and 11 distinct teeth (9-11) on each side, often a detached tooth at base. Hair 0(1), 1(1), 3(1), 4(5, 3-5), 5(4, 3-5), 6(14, 11-14), 7(5, 4-7), 8(1), 9(2, 2-3), 10(1), 11(6, 3-8), 12(2, 1-2), 13(1), 14(1), 15(2, 2-3). *Antenna*: Length about 0.45 of head; pigmentation very light; shaft with a few scattered spicules. Hair 1-A about 0.5 from base. *Thorax*: Stellate hairs with a few, unequal, weakly barbed branches; long hairs barbed and with attenuate apices. Prothorax: hair 0(12, 10-14), 1(9, 7-11), 2(1), 3(14, 8-16), 4(1, 1-2), 5(2, 2-3), 6(1), 7(2, 2-3), 8(6, 6-10), 9(1, 1-2), 10(1), 11(3, 3-5), 12(1), 14(10, 8-14). Mesothorax: hair 1(5, 3-9), 2(1), 3(1), 4(1), 5(1), 6(5, 4-5), 7(1), 8(6, 5-7), 9(8, 7-10), 10(1), 11(2, 1-2), 12(1), 13(14, 10-14), 14(4, 4-9). Metathorax: hair 1(2, 2-8), 2(1), 3(3, 3-5), 4(8, 5-9), 5(8, 6-11), 6(1), 7(7, 7-9), 8(6, 4-9), 9(8, 6-8), 10(1), 11(2, 1-3), 12(1), 13(11, 5-13). *Abdomen*: Stellate hairs as on thorax. Segment I: hair 1(5, 5-12), 2(8, 5-9), 3(1), 4(3, 2-4), 5(8, 7-11), 6(3), 7(1), 9(1), 10(1), 11(8, 7-9), 13(10, 3-12). Segment II: hair 0(1), 1(3, 2-9), 2(7, 3-8), 3(1), 4(3, 2-3), 5(9, 7-11), 6(3), 7(2, 2-3), 8(1, 1-2), 9(6, 5-7), 10(1), 11(1), 12(1), 13(8, 5-12). Segment III: hair 0(1), 1(3, 2-5), 2(7, 5-8), 3(1), 4(2), 5(10, 9-11), 6(1, 1-2), 7(6, 4-7), 8(1), 9(6, 5-7), 10(1), 11(1), 12(1), 13(9, 5-13), 14(1). Segment IV: hair 0(1), 1(3, 2-4), 2(7, 6-8), 3(1), 4(2), 5(9, 9-12), 6(1, 1-2), 7(5, 4-6), 8(1), 9(6, 5-6), 10(1), 11(1), 12(1), 13(10, 7-11), 14(1). Segment V: hair 0(1), 1(2, 2-3), 2(6, 5-7), 3(1), 4(3, 2-4), 5(10, 9-11), 6(1, 1-2), 7(5, 4-6), 8(1), 9(6, 5-6), 10(1), 11(1), 12(1), 13(8, 4-11), 14(1). Segment VI: hair 0(1), 1(2, 2-3), 2(6, 5-7), 3(1), 4(1, 1-2), 5(7, 5-10), 6(1), 7(2, 2-3), 8(3, 2-3), 9(5, 4-6), 10(1), 11(1), 12(1), 13(9, 6-11), 14(1). Segment VII: hair 0(1), 1(2, 2-4), 2(5, 4-7), 3(1), 4(1), 5(2, 2-3), 6(2, 2-3), 7(1), 8(5, 3-7), 9(4, 4-6), 10(1), 11(1), 12(1), 13(6, 3-6), 14(1). *Segment VIII*: Comb scales 18(16-19) in number, individual scale moderately pigmented, elongate and fringed on sides and apex. Hair 0(1), 1(4, 4-6), 2(1), 3(6, 5-7), 4(1), 5(4, 3-5), 14(1). *Siphon*: Index about 5.8-6.7; moderately pigmented, with darker basal ring. Pecten extending to about 0.43; 19(19-24) narrow, long teeth. Hair 1(2, 2-3), 2(1), 3-5 not visible, 6(1), 7(1), 8(2, 1-2), 9(1). *Anal Segment*: Saddle moderately pigmented. Gills subequal;

moderate, less than 2.0 of saddle length. Hair 1(1, 1-2), 2(7, 5-8), 3(1), 4a(4, 4-5), 4b(4, 3-4), 4c(4, 3-4), 4d(4), 4e(4, 3-4), 4f(3, 3-4).

SYSTEMATICS. *A. stenei* appears to be most closely related to *inaequalis*. I have not found any reliable characters to separate the adults of these 2 species and their pupae are also very similar but apparently differentiated by the features mentioned in the diagnoses and key. The larva of *stenei* is readily separated from *inaequalis* and the other members of the group. There appears to be a strong ecological barrier between *stenei*, which breeds exclusively in bromeliads, and *inaequalis*, which is primarily a treehole breeder and has never been found in bromeliads. *A. stenei* has been collected most frequently at elevations of about 1,000 feet and less commonly down to 100 feet and as high as 2,500 feet. Its most common associate is *grabhami*; as indicated under the latter there is a suggestion of occasional hybridization between these 2 forms. *A. stenei* is the most common and widespread species of the group and has been reported from all the parishes of Jamaica except Clarendon, Trelawny and Westmoreland.

BIONOMICS. *A. stenei* has been found breeding only in terrestrial and epiphytic bromeliads. Although the females of *stenei* and *inaequalis* cannot be separated with certainty, I believe that the majority of the *stenei-inaequalis* specimens collected in the 24-hour biting-landing study reported in fig.7 were probably *stenei*. These showed a small peak of activity at 1700 hrs.

DISTRIBUTION (fig.3). Endemic to the island of Jamaica where it has been reported from all the parishes except Clarendon, Trelawny and Westmoreland at elevations of 100 to 2500 ft. Material examined: 1486 specimens; 226 ♂, 380 ♀, 492 pupae, 388 larvae; 371 individual rearings (227 pupal, 102 larval, 42 incomplete).

JAMAICA. *Hanover*: Lethe, elev. 500 ft, 6 Nov 1966, O.G.W. Berlin and D.C. Watson (JA 666), 2 p♀ (666-100,101), 2 p, 2 L [UCLA]. *Manchester*: Hope Farm, 2 Sept 1945, G.A. Thompson, 1 lp♀ (450902-2); 2 Oct 1945, G.A. Thompson, 2 lp♀ (451002-10,13), 1 lp♀ paratype (451002-3), 1 lp♂, paratype (451002-2); 1 Jan 1946, G.A. Thompson, 1 lp♂, paratype (460101-20), 1 lp♀ (460101-18) [USNM]; elev. 900-1000 ft, 18 Aug 1965, W.A. Page, 1 lp♂ (240-62), 2 lp♀ (240-63, 64), 1 IP (240-65), 1 lp♀ (241-62), 7 p♂ (241-101,103,106-108,110,111), 1 p♀ (241-114), 1 IP (241-60), 2 p♂ (242-62,100), 4 p♀ (242-61,103,105,106); 10 Sept 1965, W.A. Page, 1 lp♀ (355-10), 1 p♀ (355-100), 2 ♂, 2 ♀ (JA 355), 2 ♀ (JA 356); 2 Nov 1966, O.G.W. Berlin, 3 lp♂ (661-10, 11,16), 2 p♂ (661-100,104), 3 p♀ (661-101-103), 4 IP (661-12-15), 1 ♀, 2 p, 6 l (JA 661), 3 ♀ (JA 663A); 12 Nov 1966, O.G.W. Berlin, 90 ♀ (JA 684), 3 P, 5 L (JA 685), 3 lp♂ (688-14,17,19), 2 lp♀ (688-10,18), 9 p♂ (688-105,106,112,117-119,124,125,127), 1 p♀ (688-109), 5 ♀, 1 p, 9 l (JA 688) [UCLA]. *Porus*, elev. 900-1000 ft, 23 Oct 1966, O.G.W. Berlin and D.C. Watson, 1 lp♀ (630-12), 1 IP (630-13), 1 ♂, 1 p, 3 L (JA 630), 2 lp♂ (631-13,14), 4 lp♀ (631-10,11,16,17), 4 p♂ (631-100, 101,104,107), 6 p♀ (631-102,103,110,111,114,115), 5 IP (631-18-22), 2 ♂, 1 ♀, 1 p (JA 631), 1 lp♂ (632-14), 3 p♂ (632-109-111), 1 p♀ (632-113), 1 IP (632-16), 1 ♂, 1 ♀, 2 P, 2 p, 5 L, 3 l; 1 Nov 1966, O.G.W. Berlin, 1 p♀ (655-102), 1 l (JA 655), 3 lp♀ (658-10,11,13), 6 p♂ (658-100-102,106, 109,111), 3 p♀ (658-104,105,108), 1 IP (658-12), 1 ♀, 2 p, 2 l [UCLA]. *Portland*: Kemney-Sherwood Forest, elev. 750 ft, 13 Aug 1967, J.N. Belkin and W.A. Page, 2 p♀ (706-12,103), 1 ♂, 1 ♀ (JA 706), 1 lp♀ (708-10), 1 ♂, 1 ♀, 2 p, 2 l (JA 708), 2 L (JA 710), 2 p (JA 711) [UCLA]. *St. Andrew and Kingston*: Hermitage Dam Road, 1 Sept 1965, W.A. Page (JA 319), 1 p♂ (319-102); 29 Oct 1965, W.A. Page (JA 392), 3 p♂ (392-103,107,112), 2 p♀ (392-108,110); 15 Aug 1967, J.N. Belkin and W.A. Page, 1 lp♀ (723-25), 2 p♀ (723-100,101), 1 IP (723-22), 1 ♀, 2 P (JA 723), 2 lp♂ (725-22,23), 2 lp♀ (725-11,12), 7 p♂ (725-94,101,102A,103A,108,111,112A), 9 p♀ (725-100,103, 105B,106A,107A,110,111A,113,114), 2 IP (725-20,21), 3 ♀, 1 P, 5 p (JA 725); 25 July 1967, W.A. Page, 3 p♂ (854-100,101,103), 1 p♀ (854-104), 1 lp (854-12), 1 P, 1 l (JA 854), 1 P (JA 855) [UCLA]. *Kingston*, 15 Sept 1906, M. Grabham, 1 ♂ [USNM]. *Mavis Bank*, M. Grabham, 1 ♂ [USNM]. *Mt. Salus Road*, 11 Sept 1967, W.A. Page (JA 779), 2 p♂ (779-102,106), 1 p♀ (779-103) [UCLA]. *Newcastle*, elev. 2500 ft, 29 Oct 1966, O.G.W. Berlin, 3 L (JA 648) [UCLA]. *Shooters*

Hill, elev. 1800 ft, 3 Dec 1946, G.A. Thompson, 2 ♀ [IJ]. Stony Hill, 16 Sept 1946, G.A. Thompson, 1 ♀ [IJ]. Temple Hall, elev. 500 ft, 27 Oct 1966, O.G.W. Berlin and D.C. Watson, 3 L (JA 646) [UCLA]. *St. Ann*: Moneague, 1943, R.B. Hill, 1 ♀ [USNM]; 9 Sept 1966, D.C. Watson, 1 ♂, 1 ♀ (JA 607); 17 Aug 1967, J.N. Belkin and W.A. Page (JA 733), 2 lp♂ (733-10,15), 9 lp♀ (733-11-14, 16-19,30), 7 p♂ (733-90,94,97,104,107,110,113), 12 p♀ (733-31,41,92,93,99-102,106,111,112), 12 ♂, 19 ♀, 2 P, 18 p, 11 L, 3 l; 6 Aug 1967, W.A. Page (JA 771), 1 p♀ (771-102), 1 L [UCLA]; Faiths Pen Schoolyard, elev. 1750 ft, 30 Aug 1967, W.A. Page (JA 762), 1 lp♂ (762-11), 2 lp♀ (762-12,13), 1 l♀ (762-14), 1 p♂ (762-103), 1 p♀ (762-102), 1 P, 9 L, 1 l [UCLA]; 2.0 mi S of Moneague near Unity, elev. 1750 ft, 26 Aug 1967, W.A. Page (JA 758), 1 lp♀ (758-23), 4 p♀ (758-31,32,108,111), 5 p♀ (758-105-107,112,114), 8 ♂, 6 ♀, 5 p, 15 L [UCLA]; 29.0 mi post on Moneague Road, elev. 1750 ft, 30 Aug 1967, W.A. Page, 1 lp♂ (763-20), 6 lp♀ (763-12,14,21-23,30), 8 p♂ (763-90,94,96-98,100,107,111), 6 p♀ (763-95,99,101-103,105), 2 ♂, 12 ♀, 11 P, 19 p, 18 L, 1 l (JA 763), 1 lp♂ (764-31), 1 lp♀ (764-34), 5 p♂ (764-32,96,112-114), 4 p♀ (764-90,93,107,111), 1 lp (764-33), 6 ♂, 8 ♀, 5 P, 5 p, 1 L, 1 l [UCLA]; Moneague-Claremont Road, 17 Sept 1965, W.A. Page, 1 p♂ (380-106), 1 p (JA 380), 1 lp♀ (381-12), 1 p♂ (381-100) [UCLA]; Moneague-Ocho Rios Road, 10 Sept 1967, W.A. Page (JA 776), 1 p♂ (776-100) [UCLA]. Mt. Diablo, 17 Sept 1965, W.A. Page, 2 lp♂ (375-11,14), 2 p♀ (375-10,100), 2 lp (375-15,22), 8 ♀, 2 l (JA 375), 3 lp♂ (376-10,11,13), 2 lp♀ (376-15,16), 2 p♂ (376-100,102), 3 P (JA 376); 17 Aug 1967, J.N. Belkin and W.A. Page, 1 lp♂ (731-22), 2 lp♀ (731-20,23), 1 p♂ (731-96), 1 p♀ (731-101), 1 ♂, 2 ♀, 2 p, 3 L (JA 731), 2 lp♀ (732-30,31), 4 p♂ (732-95,103,109,110), 2 p♀ (732-32,98), 1 lP (732-33), 2 P, 2 p, 7 L, 1 l (JA 732), 2 lp♀ (734-10,11), 4 p♂ (734-103,104,106,109), 3 p♀ (734-100,107,108), 1 lP (734-12), 2 ♀, 1 p, 22 L (JA 734); 7 Sept 1967, W.A. Page, 1 lp♀ (779-10), 1 p♀ (774-107), 4 L (JA 774) [UCLA]. *St. Catherine*: Bog Walk, elev. 500 ft, 12 July 1967, W.A. Page (JA 820), 1 p♂ (820-11) [UCLA]. *St. Elizabeth*: Maggoty, elev. 500 ft, 15 Sept 1967, W.A. Page (JA 791), 1 L [UCLA]. *St. James*: Five Miles, elev. 100 ft, 6 Nov 1966, O.G.W. Berlin and D.C. Watson (JA 676), 1 lp♀ (676-12), 4 p♂ (676-102,103,105,124), 8 p♀ (676-100,101,106,108,109,117,122,125), 4 ♂, 2 ♀, 2 L [UCLA]. Montego Bay, elev. 500 ft, 6 Nov 1966, O.G.W. Berlin and D.C. Watson (JA 669), 1 lp♂ (669-10), 1 lp♀ (669-11), 2 p♂ (669-100,102), 1 p♀ (669-101), 3 L, 1 l [UCLA]; 16 Jan 1940, 2 ♂, 2 ♀; 17 Jan 1940, 2 ♂, 3 ♀ [USNM]. Reading, elev. 200 ft, 6 Nov 1966, O.G.W. Berlin and D.C. Watson, 3 p♂ (670-100-102), 1 p♀ (670-103), 3 P, 3 p, 5 l (JA 670), 2 lp♀ (671-10,14), 1 p♂ (671-100), 4 lP (671-11-13,15), 13 L (JA 671), 1 p♂ (673-101), 1 p♀ (673-100), 1 lP (674-10), 1 p, 4 L (JA 674) [UCLA]. *St. Mary*: Broadgate, elev. 500 ft, 27 Oct 1966, O.G.W. Berlin and D.C. Watson (JA 643), 4 lp♂ (643-32,38-40), 3 lp♀ (643-34-36), 6 p♂ (643-104,106-108,112,113), 6 p♀ (643-30,100-103,105), 2 lP (643-41,42), 3 ♂, 2 ♀, 2 P, 3 L, 5 l [UCLA]. *St. Thomas*: Port Morant Bay, 16 Aug 1967, J.N. Belkin and W.A. Page (JA 729), 3 lp♂ (729-10,11,20), 1 p♂ (729-102), 4 p♀ (729-100,101,103,104), 7 L, 2 l [UCLA]. Windsor Forest, elev. 750 ft, 30 Oct 1966, O.G.W. Berlin and D.C. Watson, 1 lp♀ (650-24), 3 p♂ (650-104,106,107), 1 p♀ (650-108), 1 lP (650-20), 3 ♂, 2 ♀, 2 L, 2 l (JA 650), 1 lp♂ (651-37), 2 lp♀ (651-35,39), 4 p♂ (651-110-113), 1 p♀ (651-114), 5 lP (651-31-33,36,38), 1 p, 1 l (JA 651), 2 lp♂ (652-11,13), 2 p♂ (652-106,109), 2 p♀ (652-105,107), 3 L, 2 l (JA 652) [UCLA]. *Parish not specified*: New Park, June 1929, C.D. Williams, 1 ♀ [BM]. Apr 1906, M. Grabham, 1 ♀; 1944, R.B. Hill, 4 ♂, 1 ♀; Jan 1940, W.H.W. Komp, 2 ♂; R.B. Hill, 1 ♂, 4 ♀ [USNM]; W.A. Page, 2 lp♂ (771-10,12), 3 p♂ (771-100,104,107), 3 p♀ (771-13,102,105), 1 P, 1 p, 28 L (JA 771), 2 lp♀ (772-32,35), 2 p♂ (772-100,112), 2 p♀ (772-102,105), 2 ♂, 5 ♀, 2 P, 3 p, 15 L (JA 772) [UCLA].

Ioliota Group

FEMALES. *Head*: Narrow decumbent scales white. Palpus with apical silvery white scales. *Thorax*: Inner dorsocentral line narrow, pale golden; median prescutellar line broad, white; outer dorsocentral line narrow, pale golden; lateral marginal line narrow, white, nearly continuous from anterior promontory to wingbase. Acrostichal bristles not developed on disc. Scutellum predominantly dark scaled, light

scales restricted to median lobe. *Ssp* with distinct silvery patch; upper *stp* patch separate, small. *Legs*: Foretarsus with a few white scales on base of segment 2; midtarsus with small incomplete basal white rings on segments 1,2; hindtarsus with broader complete basal white rings on segments 1-3 and with segment 5 completely or largely white. *Abdomen*: Basomedian tergal white markings dingy white or creamy on segments III-VI or V-VI, white on VII.

MALES. Palpus with submedian white scales on segments 4,5. Larger claw of foreleg and midleg with small acute basal tooth and large blunt submedian tooth; smaller claw with basal tooth only.

MALE GENITALIA. Claspette with short broad conical tubercle bearing 1 or rarely 2 apical bristles. Clasper less than 0.5 of sidepiece; with distinct subapical hairs. Aedeagus subquadrate, shorter than proctiger.

PUPAE. *Cephalothorax*: Hair 5-C single or double, at least 2.0 of hair 4-C; hair 7-C usually single; hair 10-C single to triple. *Abdomen*: All large hairs except 1-II,III, 9-VII,VIII usually single or double; hair 2-II laterad of or in line with hair 3; hair 5-IV,V short to moderate, not exceeding middle of tergite following; hair 9-II-VI caudad of hair 6; 9-VII longer, stouter and with more branches than hair 6-VII. *Paddle*: Moderate; apex rounded; marginal spicules indistinct.

LARVAE. *Head*: Hair 1-C unbranched; 4-C moderately long, multiple; 5,6-C both long, single; hairs 11,14-C weakly stellate, 11-C with unequal branches; 15-C double, long, exceeding apex of mental plate. *Antenna*: Shaft with a few minute sharp spicules; hair 1-A single. *Thorax*: Hair 13-P present. Hairs 0,8,13,14-P, 1,4,5,8,13-T weakly stellate; hair 1-T far mesad of hairs 2,3. *Abdomen*: Integument glabrous dorsally, ventral surfaces of segments II-VIII with rows of minute spinelike spicules; hair 2 distinctly removed cephalad but not beyond hair 8, hair 9 not markedly displaced cephalad. Hairs 2,5-I-VI, 9-II-VI, 11-I distinctly stellate, with a few branches, 2,9,11 distinctly heavier than others, hairs 1-I,II, 7-III-VI, 9-I very weakly stellate; hair 8-VII distinctly cephalodorsad of 9-VII. *Segment VIII*: Comb scales in a single row; individual scales moderate in length, blunt apically and finely fringed. *Siphon*: Index less than 3.0; integument without spicules; distinct attached acus present. Pecten extending to about middle of siphon, not reaching hair 1-S; teeth numerous, closely set, with basal denticles. *Anal Segment*: Saddle body without distinct spicules; caudal margin with short pointed spines preceded by a few rows of spicules; hair 1-X usually single (1-3), near lower end of caudal margin. Ventral brush with 6 pairs of hairs on a small sclerotized boss with distinct grid bars.

DISCUSSION. The Ioliota Group of 2 very similar species is most strikingly differentiated from the other groups of the section by the presence of hair 13-P in the larva, a character not found anywhere else in the section. In adult ornamentation this group is very similar to the Albonotatus Group, differing from it primarily in the presence of light scaling on hindtarsal segment 5.

The 2 species have widely disjunct distributions, *cozumelensis* occurring only on the Yucatan Peninsula and the adjacent Cozumel island and British Honduras, and *ioliota* at the opposite end of the Caribbean sea in northern Venezuela and Trinidad (fig.3). The 2 species are so similar that they obviously belong to the same phylad. Their pattern of distribution is interpreted here as a relict of a former wide distribution of the group in the central Caribbean area. A similar pattern is found in the Walkeri Group.

A larva in a recent collection from a cut bamboo from the province of Guayas (ECU 161) indicates the presence of another member of the Ioliota Group in Ecuador. It differs from other members of the group by a 14-16 branched stellate hair

13-P which is only 3-5 branched in *ioliota* and double in *cozumelensis*. The *albonotatus* of Levi-Castillo (1952a:77; 1952b:555; 1953:40) is probably this member of the *Ioliota* Group.

Both members of the group were probably originally treehole breeders. They have been reported primarily from artificial containers and *ioliota* has been found breeding in fallen cacao pods. There are no records of this group from bromeliad axils.

12. *Aedes* (*Howardina*) *ioliota* Dyar and Knab

Figs. 3, 8, 27, 28

1913. *Aedes ioliota* Dyar and Knab, 1913:76-78. TYPE: Holotype ♀, Trinidad, locality not specified, F.W. Urich [USNM, 16000].

Aedes (*Howardina*) *ioliota* of Bonne and Bonne-Wepster (1925:371-372); Dyar (1928:233); Edwards (1932:155); Lane (1939:100; 1953:719-720); Anduze (1941:14); Horsfall (1955:471); Stone and Knight (1956:219-220); Stone, Knight and Starcke (1959:174); Aitken (1960:4); Suarez and Cova Garcia (1961:17-24); Stone (1963:127); Belkin, Schick and Heinemann (1965:69); Forattini (1965:401); Cova Garcia, Sutil and Rausseo (1966a:57,283; 1966b:73-74,141,169,334).

Aedes ioliota of Urich (1913:528); Dyar (1918:73).

FEMALE. Wing: 3.33 mm. Proboscis: 2.62 mm. Forefemur: 2.45 mm. Abdomen: about 2.98 mm. As described for the group, with following apparently diagnostic features. *Head*: Median stripe on vertex narrow, white; light scales on sides and venter straw yellow. Erect scales dark brown. Palpus about 0.16 of proboscis. *Thorax* (fig. 3): Scales on anterior promontory white. Inner dorsocentral line narrow, creamy, reaching prescutellar space, followed by a moderate, white-scaled median prescutellar line; outer dorsocentral line narrow, golden; lateral marginal line white, narrow, long, extending from side of anterior promontory to wingbase, apparently interrupted only at scutal angle. Antealar area above paratergite with scattered dark scales. Light scales on median scutellar lobe narrow, white; lateral lobes with a few narrow dark scales. Pleural scales as in the section and group. *Legs*: Forefemur and midfemur predominantly dark anteriorly, a few basal scales creamy, proximal 0.5 of posterior surface straw yellow, extending distally as a narrow line, rest dark; hindfemur predominantly straw yellow to 0.5 on both sides, rest dark scaled. Hindtarsal segment 5 completely white scaled. *Haltere*: Stem pale, knob mostly whitish, a few dark scales dorsally. *Abdomen*: Sternites predominantly creamy on II, III; rest with basal creamy and apical dark scales, latter increasing in extent on distal segments.

MALE. Wing: 2.79 mm. Proboscis: 2.54 mm. Forefemur: 1.93 mm. Essentially similar to female in coloration.

MALE GENITALIA (fig. 27). As figured; diagnostic characters as in the key. Ninth tergite lobe prominent, with 5, 6 strong bristles. Sidepiece length about 2.5 median width; basolateral scales white, remainder dark. Claspette with 2, 3 small subapical hairs. Clasper about 0.5 of sidepiece, with 1 subapical hair; minute spicules on basal 0.5. Dorsal sclerotization of aedeagus very shallowly emarginate, but without distinct lateral lobes.

PUPA (fig. 27). Abdomen: 3.35 mm. Trumpet: 0.43 mm; index 4.4-4.6. Paddle: 0.74 mm. Chaetotaxy as given below, hairs moderately to darkly pigmented. Diagnostic characters as in the key. Apparently distinguished from *cozumelensis* by the

more dendritic hair 1-II and longer, ovoid or slightly produced paddle, with length about 1.5 greatest width. *Cephalothorax*: Mesonotum moderately pigmented between trumpets, lateral areas and metanotum deeply pigmented; trumpets strongly contrasting. Hair 1(1), 2(2, 1-2), 3(1), 4(2, 1-3), 5(1, 1-2), 6(1), 7(1), 8(3, 2-4), 9(1), 10(2, 1-3), 11(1, 1-2), 12(1, 1-3). *Abdomen*: Tergite I moderately pigmented except for usual membranous areas; segments II and III imbricate, moderately pigmented; rest of segments progressively lighter caudad. Segment I: hair 1(6-12 primary branches, each with many secondary ones), 2(1), 3(1), 4(3, 2-4), 5(2, 2-3), 6(1), 7(1), 9(1). Segment II: hair 0(1), 1(3, strongly dendritic), 2(1, 1-2), 3(1, 1-2), 4(4, 2-5), 5(1), 6(1), 7(1), 9(1). Segment III: hair 0(1), 1(2, 1-4), 2(1), 3(1), 4(2, 1-4), 5(1), 6(1), 7(2, 1-4), 8(2, 1-3), 9(1), 10(1, 1-2), 11(1), 14(1). Segment IV: hair 0(1), 1(1, 1-3), 2(1), 3(3, 1-4), 4(1, 1-2), 5(1), 6(1), 7(2, 1-3), 8(2, 1-2), 9(1), 10(2, 1-3), 11(1), 14(1). Segment V: hair 0(1), 1(1, 1-3), 2(1), 3(1, 1-2), 4(4, 2-5), 5(1), 6(1), 7(3, 1-4), 8(2, 1-3), 9(1), 10(1), 11(1), 14(1, 1-2). Segment VI: hair 0(1), 1(1, 1-2), 2(1), 3(1, 1-2), 4(2, 1-3), 5(1), 6(1), 7(1), 8(2, 1-3), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1), 6(2, 1-4), 7(1, 1-2), 8(2, 1-2), 9(3, 2-4), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(5, 4-6), 14(1, 1-2). *Paddle*: Uniformly lightly pigmented, midrib slightly darker; moderately elongate and oval, sometimes slightly produced; external margin smooth; hair 1-P slender. Male genital lobe extending to 0.47 of paddle, female genital lobe to 0.38.

LARVA (fig.28). Head: 0.88 mm. Siphon: 0.86 mm. Anal Saddle: 0.34 mm. Chaetotaxy as given below, hairs moderately to darkly pigmented; in life, larvae are dark. Diagnostic characters as in the key; readily separated from *cozumelensis* by the apically rounded comb scales and hair 1-X single. *Head*: Width about 1.1 of length; integument strongly pigmented. Mental plate with strong median tooth and 10(9-11) distinct teeth on either side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(13, 12-16), 5(1), 6(1), 7(2, 2-3), 8(1, 1-2), 9(1, 1-2), 10(1), 11(6, 4-7), 12(2, 2-3), 13(1, 1-2), 14(3, 3-7), 15(2, 2-3). *Antenna*: Length about 0.33 of head; uniformly strongly pigmented. Hair 1-A about 0.54 from base. *Thorax*: Long hairs with attenuate apices; long and stellate hairs weakly barbed. Prothorax: hair 0(7, 5-9), 1(3, 2-3), 2(1), 3(4, 3-5), 4(3, 3-5), 5(2, 2-3), 6(1), 7(3, 2-3), 8(6, 5-7), 9(1), 10(1), 11(1, 1-2), 12(1), 13(4, 3-5), 14(20, 18-24). Mesothorax: hair 1(5, 4-6), 2(1), 3(1), 4(1), 5(1), 6(4, 4-5), 7(1), 8(5, 4-6), 9(6, 4-7), 10(1), 11(2, 1-2), 12(1), 13(6, 5-9), 14(5, 3-5). Metathorax: hair 1(4, 4-6), 2(1), 3(2, 1-3), 4(6, 3-6), 5(7, 6-8), 6(1), 7(6, 5-7), 8(5, 4-7), 9(5, 3-6), 10(1), 11(1, 1-2), 12(1), 13(6, 5-7). *Abdomen*: Long and stellate hairs as on thorax. Segment I: 1(4, 4-6), 2(6, 5-7), 3(1), 4(3, 1-4), 5(7, 5-10), 6(3, 2-5), 7(1), 9(4, 3-5), 10(1), 11(6, 6-8), 13(3, 3-5). Segment II: hair 0(1), 1(4, 3-6), 2(6, 6-7), 3(1), 4(2, 2-4), 5(7, 6-9), 6(3), 7(4, 3-4), 8(1, 1-2), 9(6, 4-7), 10(1), 11(1), 12(1), 13(5, 3-5). Segment III: hair 0(1), 1(3, 3-5), 2(7, 6-8), 3(1), 4(1), 5(7, 5-10), 6(2), 7(4, 3-5), 8(1), 9(7, 5-7), 10(1), 11(1), 12(1), 13(3, 3-6), 14(1). Segment IV: hair 0(1), 1(4, 1-4), 2(6, 6-7), 3(1), 4(1), 5(8, 6-9), 6(2), 7(4, 3-5), 8(1), 9(6, 5-8), 10(1), 11(1), 12(1), 13(4, 3-4), 14(1). Segment V: hair 0(1), 1(2, 1-4), 2(6, 6-7), 3(1), 4(1, 1-2), 5(7, 6-8), 6(2), 7(4, 3-5), 8(1, 1-2), 9(4, 4-7), 10(1), 11(1), 12(1), 13(3, 2-4), 14(1). Segment VI: hair 0(1), 1(4, 2-5), 2(6, 5-7), 3(1), 4(1), 5(6, 5-8), 6(2, 1-2), 7(3, 2-3), 8(2, 1-2), 9(5, 4-6), 10(1), 11(1), 12(1), 13(3, 3-4), 14(1, 1-2). Segment VII: hair 0(1), 1(2, 2-4), 2(6, 5-7), 3(1), 4(1), 5(6, 5-7), 6(2, 2-4), 7(1), 8(4, 3-5), 9(3, 2-4), 10(1), 11(1), 12(1), 13(2, 1-3), 14(1, 1-3). *Segment VIII*: Comb scales in a single row, 16(14-19) in number; individual scale moderate, blunt apically and finely fringed. Hair 0(1), 1(6, 5-7), 2(1), 3(7, 5-8), 4(1), 5(4, 3-5), 14(1, 1-2). *Siphon*: Index about 2.3-2.7; darkly pigmented, imbricate. Pecten extending to 0.46;

teeth 14(12-17); smaller basally, progressively larger distad; individual tooth with a long spine and a basal denticle. Hair 1(3, 2-3), 2(1), 3-5 not visible, 6(1), 7(1), 8(1), 9(1). *Anal Segment*: Saddle darkly pigmented, imbricate. Gills short, broad, unequal, ventral 0.67 of dorsal. Hair 1(1, 1-3), 2(5, 4-6), 3(1), 4a(4, 4-6), 4b(4, 3-4), 4c(4, 3-4), 4d(4, 3-5), 4e(3, 3-4), 4f(3, 1-3).

SYSTEMATICS. *A. ioliota* is extremely similar to *cozumelensis* from which it is differentiated apparently only by the few constant diagnostic characters mentioned above. There is no indication of any differentiation between the populations from Trinidad and Venezuela. This species is apparently restricted to low and moderate elevations in the Cordillera de la Costa in Venezuela and in Trinidad but may be present in the intermediate area.

BIONOMICS. The reported breeding sites of *ioliota* are quite varied, ranging from rockholes, treeholes, broken and cut bamboo to fallen cacao fruits and artificial containers of varied size. Females have been taken in biting-landing collections (TR 1132). Attempts at experimental infection with yellow fever virus have yielded negative results (Aitken 1960:4).

DISTRIBUTION (fig.3). Trinidad and Venezuela (northern) at low to moderate elevations. Material examined: 115 specimens; 15 ♂, 23 ♀, 30 pupae, 47 larvae; 30 individual rearings (12 pupal, 15 larval, 3 incomplete).

TRINIDAD. *St. Andrew*: Cumaca, elev. 250 ft, 22 Oct 1964, rockhole, A. Guerra (TR 783), 1 lp♂ (783-104), 2 lp♀ (783-103,105); elev. 500 ft, 14 Jan 1965, tub, A. Guerra (TR 940), 3 lp♂ (940-120,121,129), 3 lp♀ (940-110,113,125), 1 p♀ (940-111), 3 IP (940-114,122,123), 12 L; 18 Feb 1965, tin can, A. Guerra, 1 lp♀ (1008-21), 1 p♂ (1008-20), bamboo pot, 2 p♂ (1013-10,11), 1 p♀ (1013-13), 5 L (TR 1013) [UCLA]; Cumaca Road, elev. 500 ft, 14 Jan 1965, fallen cacao pod, A. Guerra (TR 938), 4 lp♀ (938-128-131), 8 L [UCLA]. *St. George*: Mt. Beck, elev. 1000 ft, 29 Apr 1965, biting collection, A. Guerra, 1 ♀ (TR 1132) [UCLA] *County not specified*: F.W. Ulrich, 3 ♀, type series [USNM no. 16000].

VENEZUELA. *Aragua*: Choroní, Mar 1939, P.J. Anduze, 1 ♂ [USNM]. Guamito, 19 June 1927, M.N. Tovar, 1 ♀; 4 July 1927, M.N. Tovar, 1 ♀ [USNM]; 1 Dec 1967, cut bamboo, R. Hansell and J.J. Vera (VZ 83), 1 lp♂ (83-13), 3 p♂ (83-101,105,106), 1 p♀ (83-102), 4 L [UCLA]. Maracay, 4 July 1927, M.N. Tovar, 1 p♂ [USNM]. Ocumare de la Costa, 12 Aug 1927, M.N. Tovar, 1 ♀ [USNM]. Colonia Tovar, Capital, Guamitas, Rancho Grande and Uraca (Cova Garcia, Sutil and Rausseo 1966b:73). *Carabobo*: Las Trincheras (Cova Garcia, Sutil and Rausseo 1966b:73). *Falcon*: Cumarebo (Cova Garcia, Sutil and Rausseo 1966b:73). *Miranda*: Carenero and Charallave (Cova Garcia, Sutil and Rausseo 1966b:74). Hacienda Los Chaguaramos (Suarez and Cova Garcia 1961: 17; Cova Garcia, Sutil and Rausseo 1966b:74). Los Teques and Petare (Cova Garcia, Sutil and Rausseo 1966b:74). *Trujillo*: Sabana de Mendoza (Cova Garcia, Sutil and Rausseo 1966b:74).

13. *Aedes* (Howardina) *cozumelensis* Diaz Najera

Figs.3,8,29,30

1966. *Aedes* (Howardina) *cozumelensis* Diaz Najera, 1966a:331-344. TYPE: Holotype ♂ with genitalia slide, San Miguel de Cozumel, Territorio de Quintana Roo, Mexico, 25 Sept 1965, A. Diaz Najera [ISET, 6529].

Aedes (Howardina) *cozumelensis* of Stone (1967:208).

FEMALE. Wing: 3.5 mm. Proboscis: 2.98 mm. Forefemur: 2.28 mm. Abdomen: about 2.5 mm. Very similar to *ioliota* in color and size, differing apparently only in the following (fig.8). Hindtarsal segment 5 with some apical and posterior dark scales, rest white.

MALE. Wing: 3.15 mm. Proboscis: 2.45 mm. Forefemur: 2.01 mm. Essentially similar to female in coloration.

MALE GENITALIA (fig.29). As figured; diagnostic characters as in the key. Ninth tergite lobe indistinct, with 4,5 strong setae. Sidepiece length about 3.0 median width. Claspette with 1 apical seta and varied number of smaller subapical setae, progressively smaller basally. Clasper about 0.5 of sidepiece, with 1,2 subapical hairs; basal 0.5 with spicules.

PUPA (fig.29). Abdomen: 3.78 mm. Trumpet: 0.55 mm; index about 4.1. Paddle: 0.74 mm. Description based on a single skin. Diagnostic characters as in the key. Apparently differing from *ioliota* by hair 1-II with a few simple branches and paddle shorter, length about 1.2 greatest width. *Cephalothorax*: Mesonotum moderately pigmented between trumpets, lateral areas and metanotum strongly pigmented; trumpets strongly contrasting. Hair 5-C strong, at least 2.0 as long as 4-C. *Abdomen*: Tergite I strongly pigmented except for usual membranous areas; segments II-IV strongly pigmented; rest of segments progressively lighter caudad. All large hairs except 1-II, 9-VII,VIII usually single or double; hair 1-II not distinctly dendritic and with about 8 branches. *Paddle*: Uniformly moderately pigmented, midrib slightly darker; slightly broadened in distal half; external margin with submarginal serrations. Male genital lobe extending to about 0.5 of paddle, female genital lobe to 0.36.

LARVA (fig.30). Head: 0.76 mm. Siphon: 0.65 mm. Anal Saddle: 0.27 mm. Description based on a single specimen. Diagnostic characters as in the key. Hairs moderately to strongly pigmented. Readily separated from *ioliota* by the apically pointed comb scales and hair 1-X double. *Head*: Hairs and branching as in *ioliota*. Mental plate with a strong median tooth and 10 distinct teeth on either side, a smaller detached tooth at base. *Antenna*: Slender, moderate; strongly pigmented. Hair 1-A at about 0.56 from base. *Thorax*: Hair 13-P double. *Segment VIII*: Comb scales in a single row, 14 in number; individual scale moderate, pointed apically and fringed. *Siphon*: Index about 2.0; imbricate, moderately pigmented, with darker basal ring. Pecten extending to 0.6; teeth 15,16; individual tooth with long spine and a small basal denticle. *Anal Segment*: Saddle imbricate, moderately pigmented and with darker basal ring. Gills short, broad, unequal, ventral about 0.64 of dorsal.

SYSTEMATICS. *A. cozumelensis* is obviously very closely related to *ioliota* from which it is separated in all stages apparently only by the few constant features mentioned in the diagnosis. This species is known from the Yucatan Peninsula and the adjacent Cozumel Island and British Honduras.

BIONOMICS. The immature stages of *cozumelensis* have been found only in artificial containers but it is very likely that the natural breeding sites of this species are similar to those of the closely related *ioliota*. Adults of *cozumelensis* have been collected at dusk on human bait in British Honduras.

DISTRIBUTION (fig.3). Yucatan Peninsula and adjacent islands in Mexico (states of Quintana Roo and Yucatan) and British Honduras. Material examined: 11 specimens; 1 ♂, 8 ♀, 1 pupa, 1 larva; no individual rearings.

BRITISH HONDURAS. *Cayo*: Georgeville, elev. 300 ft, 27 July 1967, D.S. Bertram, biting collections, 1 ♀ (BH A369); 1 Aug 1967, D.S. Bertram, 3 ♀ (BH A339) [UCLA]. Roaring Creek, elev. 70 ft, 27 July 1967, biting collections, D.S. Bertram, 1 † (BH A339); 3 Aug 1967, D.S. Bertram, 1 ♀ (BH 376); 9 Aug 1967, D.S. Bertram, 1 ♀ (BH 427) [UCLA].

MEXICO. *Quintana Roo*: Cozumel Island, 25 Sept 1965, A. Diaz Najera, holotype ♂ (6529), 1 paratype ♀, 1 p. *Yucatan*: Tizimin, 8 Dec 1960, M. Munoz, 1 L [ISET].

Albonotatus Group

FEMALES. *Head*: Narrow decumbent scales white. Palpus with a few apical silvery white scales. *Thorax*: Inner dorsocentral line narrow, creamy; median prescutellar line broad, white; outer dorsocentral line narrow, pale golden; lateral marginal line narrow, silvery white, extending from side of anterior promontory to wingbase. Acrostichal bristles not developed on disc. Scutellum predominantly dark scaled, light scales restricted to median lobe. *Ssp* with distinct silvery patch; upper *stp* patch separate, small. *Legs*: Foretarsus with a few basal white scales on segment 2; midtarsus with small incomplete basal white rings on segments 1,2; hindtarsus with broader complete basal white rings on segments 1-3. *Abdomen*: Basomedian tergal light markings creamy on segments II-VII or III-VII.

MALES. Palpus with basomedian white scales on segments 4,5. Larger claw of foreleg and midleg with small acute basal tooth and large blunt submedian tooth; smaller claw simple.

MALE GENITALIA. Claspette represented by a basomesal tubercle bearing 1 apical bristle. Clasper subequal to or definitely shorter than sidepiece; subapical hairs not developed. Aedeagus ovate, subequal to proctiger.

PUPAE. *Cephalothorax*: Hair 5-C double to 4-branched, subequal to hair 4-C and distinctly shorter than distance from its base to that of trumpet; hair 7-C simple to triple; hair 10-C single to 5-branched. *Abdomen*: All large hairs except 1-II,III, 9-VII, VIII usually single or double; hair 2-II laterad of or in line with hair 3; hair 5-IV,V short, not exceeding apex of tergite following; hair 9-II-VI varied in position; 9-VII longer, stouter and with more branches than 6-VII. *Paddle*: Very long or moderate; apex rounded or slightly emarginate; marginal spicules distinct.

LARVAE. *Head*: Hair 1-C unbranched; 4-C moderately long, multiple; 5-C single, long; 6-C usually double, strong; none of the ventral hairs stellate; 14-C with a few spikelike branches; 15-C double, long, exceeding apex of mental plate. *Antenna*: Shaft without distinct spicules; hair 1-A very thin, single. *Thorax*: Hair 13-P absent. Only hairs 8,13-P distinctly stellate; hair 1-T far mesad of hairs 2,3. *Abdomen*: Integument glabrous; hair 2 distinctly displaced cephalad but not beyond hair 8, hair 9 not markedly displaced cephalad. Only hairs 2,9-I-VI, 11-I distinctly stellate, with a few spikelike branches; hair 8-VII distinctly cephalad of 9-VII. *Segment VIII*: Comb scales in a single or partial double row; individual scales rather short, blunt and faintly fringed. *Siphon*: Index less than 2.5; integument without spicules; distinct free or attached acus present. Pecten not extending beyond middle of siphon; teeth numerous, closely set and with basal denticles. *Anal Segment*: Saddle body without distinct spicules; caudal margin with very short pointed spines preceded by a few spicules; hair 1-X usually double (1-3), near lower end of caudal margin. Ventral brush with 6 pairs of hairs on a moderately or strongly sclerotized boss with distinct grid bars, 1 or 2 hairs usually detached.

DISCUSSION. The 2 very similar species of the Albonotatus Group are strikingly differentiated from each other by male genitalic characters, an unusual occurrence in the subgenus. The group is very similar in adult ornamentation to the Ioliota Group, differing from it primarily in having hindtarsal segment 5 completely dark. The larvae of the Albonotatus Group lack hair 13-P which is present in the Ioliota Group. Since the loss of hair 13-P is a derived feature it appears that the Albonotatus Group was probably derived from the Ioliota Group.

The Albonotatus Group has a distribution complementary to that of the Busckii Group (fig.3). *A. albonotatus* has been reported from Hispaniola (Haiti and Domini-

can Republic) and doubtfully from Guadeloupe, and *bahamensis* from the Bahamas (Grand Bahama and New Providence). As indicated under *albonotatus*, a third species of the group may be present in the Dominican Republic.

The natural breeding sites of the group are probably treeholes and broken bamboo, as has been reported for *albonotatus*. To date *bahamensis* has been found only in artificial containers.

14. *Aedes* (*Howardina*) *albonotatus* (Coquillett)

Figs. 3, 8, 31

1905. *Gymnometopa albonotata* Coquillett, 1905:183. TYPE: Lectotype ♂ (141.3) with associated larval and pupal skins, San Francisco Mts., Santo Domingo [Dominican Republic], 3 Sept 1905, A. Busck [USNM, 8297; selection of Stone and Knight, 1956:213].

Aedes (*Howardina*) *albonotatus* of Dyar (1928:233-234); Edwards (1932:155); Gerry (1932:40); Lane (1939:98; 1953:717-719); Horsfall (1955:471); Stone and Knight (1956:213); Stone, Knight and Starcke (1959:173); Belkin, Schick and Heinemann (1965:18); Forattini (1965:461); Porter (1967:38).

Aedes (*Howardina*) *albonotata* of Bonne and Bonne-Wepster (1925:369-370).

Aedes albonotata of Dyar and Knab (1906b:190, 196); Dyar (1906:15); Howard, Dyar and Knab (1912:70; 1917:618, 619, 834-835); Dyar (1918:73, 80); Root (1927:465).

Gymnometopa albonotata of Coquillett (1906b:25); Theobald (1907:211; 1910:219); Surcouf and Gonzalez-Rincones (1911:212, 213).

Haemagogus albonotata of Dyar and Knab (1906a:166).

FEMALE. Wing: 2.9 mm. Proboscis: 2.1 mm. Forefemur: 1.91 mm. Abdomen: about 2.98 mm. As described for the group, with following apparently diagnostic features. *Head*: Median stripe on vertex narrow, white; light scales on sides and venter straw yellow. Erect scales predominantly dark, a few median ones whitish. Palpus about 0.14 of proboscis. *Thorax* (fig. 8): Scales on anterior promontory white. Inner dorsocentral line narrow, creamy, reaching prescutellar space, followed by a white-scaled median prescutellar line; outer dorsocentral line narrow, golden; lateral marginal line narrow, pure white, extending from sides of anterior promontory to wing-base, apparently interrupted only at scutal angle. Antealar area above paratergite with scattered dark scales. Light scales on median scutellar lobe narrow, white; lateral lobes with a few narrow bronzy scales. Pleural scales as in the section and group. *Legs*: Forefemur and midfemur predominantly dark, a few basal scales creamy, proximal 0.5 of posterior surface mostly straw yellow, extending distally as narrow line, rest dark; hindfemur straw yellow to proximal 0.5 on both sides, rest dark scaled. Hindtarsal segment 3 white scaled in at least basal 0.7. *Haltere*: Stem pale, knob mostly whitish, a few dark scales dorsally. *Abdomen*: Basomedian tergal light scales dingy white on II-VII. Sternites straw yellow to segment IV; rest with basal straw yellow and apical dark scales.

MALE. Wing: 2.28 mm. Proboscis: 1.93 mm. Forefemur: 1.49 mm. Essentially similar to female in coloration.

MALE GENITALIA (fig. 31). As figured; diagnostic characters as in the key. Ninth tergite lobe prominent, with 4 strong bristles. Sidepiece length about 3.0 median width; most tergomesal bristles parallel to longitudinal axis. Clasper narrow, long, subequal to sidepiece; spiniform about 0.2 of clasper. Dorsal sclerotization of aedeagus slightly emarginate.

PUPA (fig.31). Abdomen: 2.7 mm. Trumpet: 0.35 mm; index 4.5. Paddle: 0.7 mm. Chaetotaxy as given below. Diagnostic characters as in the key. Readily separated from *bahamensis* by longer paddle, hair 7-C single and 9-VIII only 3-branched. *Cephalothorax*: Mesonotum and metanotum lightly pigmented; trumpets contrasting. Hair 1(1), 2(2), 3(1, 1-2), 4(2, 2-3), 5(2, 2-3), 6(1), 7(1), 8(2), 9(1), 10(1), 11(1), 12(1, 1-2). *Abdomen*: Tergite I lightly pigmented except for usual membranous areas; pigmentation of other segments progressively lighter caudad. Segment I: hair 1(9-13 primary branches, each with many secondary ones), 2(1), 3(1), 4(6, 2-8), 5(2, 1-2), 6(1), 7(1), 9(1). Segment II: 0(1), 1(2, 2-3), 2(1), 3(1), 4(2, 1-3), 5(1, 1-2), 6(1), 7(1, 1-2), 9(1). Segment III: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(2, 2-3), 5(1), 6(1), 7(2, 1-3), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment IV: hair 0(1), 1(2, 1-2), 2(1), 3(1, 1-2), 4(2), 5(2), 6(1), 7(2, 1-2), 8(1), 9(1), 10(1), 11(1), 14(1). Segment V: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1, 1-2), 5(1), 6(1), 7(2, 1-2), 8(2, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1), 6(1), 7(1), 8(2, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1), 6(1), 7(1), 8(1), 9(2, 2-3), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(3), 14(1). *Paddle*: Long; uniformly lightly pigmented, midrib slightly darker; external margin serrated; hair 1-P slender. Male genital lobe extending to 0.55 of paddle, female genital lobe to 0.34.

LARVA (Description based on Howard, Dyar and Knab, 1917:853; only fragments of two individual rearings seen). Diagnostic characters as in the key. Readily separated from *bahamensis* by the subequal gills and nature of the comb scales. *Head*: Width slightly greater than length. Mental plate broadly triangular, with a median tooth and 12 distinct teeth on either side. *Antenna*: Slender, moderate, uniform; all hairs single. *Thorax*: Rounded, wider than long. *Abdomen*: Moderate, anterior segments shorter. *Segment VIII*: Comb scales in a single row of about 15; individual scale elongate, rounded at tip and with small spinules. *Siphon*: Short, tapered on outer half, with an index of about 2.0. Pecten extending beyond middle, hair 1-S just within the last tooth; individual tooth with long spine and a small basal denticle. *Anal Segment*: Saddle as long as wide; caudal margin fringed with spines. Gills about 2.0 length of anal segment; broad and saclike, ventral pair subequal to dorsal.

SYSTEMATICS. In spite of the very limited material available and the very close similarity in the ornamentation of the adults, I consider *albonotatus* to be undoubtedly a species distinct from *bahamensis*. The male genitalia of the 2 species are markedly differentiated and the immature stages are also obviously distinct.

A. albonotatus has been reported from Haiti, Dominican Republic, Bahamas and Guadeloupe (Stone, Knight and Starcke 1959:173). I have not seen specimens from Haiti but this record may be correct as the type locality of *albonotatus* is in the Dominican Republic, also on the island of Hispaniola. The record from the Bahamas is based on a single female from New Providence which in my opinion is *bahamensis* (see). The male from Guadeloupe collected by Busck [USNM] is unquestionably *albonotatus* and it is possible that this species does occur on this island. However, no additional specimens of *albonotatus* have been found in extensive surveys on Guadeloupe in recent years and the possibility exists, particularly in view of the extreme similarity of this specimen with males from the type series of *albonotatus* from the Dominican Republic, that an error occurred in labeling Busck's material and that this Guadeloupe specimen was actually part of this type series. In addition to the type series I have seen 2 females from the Dominican Republic, near Sanchez [USNM], which differ from the former in the presence of some pale scales on the remigium of the wing. These females are only tentatively identified as *albonotatus* since they are

from the northern part of the complex island of Hispaniola and there is a possibility that another species of the group may occur there.

The record of *albonotatus* from Ecuador (Levi-Castillo 1952a:77; 1952b:555; 1953:40) is probably based on a misidentification of an undescribed species of the *Ioliota* Group (see).

BIONOMICS. The type series of *albonotatus* was reared from larvae and pupae collected in bamboo stumps.

DISTRIBUTION (fig.3). Island of Hispaniola (Haiti and Dominican Republic) and doubtfully Guadeloupe. Material examined: 17 specimens; 5 ♂, 6 ♀, 4 pupae, 2 larvae; 4 individual rearings (2 pupal, 2 larval).

DOMINICAN REPUBLIC. Sanchez, 5 Apr 1949, J.M. Brennan, 2 ♀ [USNM]. San Francisco Mts, Sept 1905, bamboo, A. Busck, 1 lp♂ (141-2), 1 lp♀ (136-2), 1 p♂ (136-3), 1 p♀ (141-7), 1 ♂ (141), 1 ♂, 1 ♀ (136), 1 ♀ [USNM, UCLA].

?**GUADELOUPE.** July 1905, A. Busck, 1 ♂ [USNM].

HAITI. Mt. Cabrite, 12 Oct 1924, W.A. Hoffman (Root 1927:465).

15. *Aedes* (*Howardina*) *bahamensis* Berlin, n.sp.

Figs.3,8,32,33

TYPES: Holotype ♂ (BAH 1) with genitalia slide, village of Hunter, Grand Bahama, Bahama Islands, 28 Nov 1964, A. Spielman and A.E. Weyer, from colony established from larvae collected in artificial containers [USNM]. Allotype ♀ (BAH 1), same data as holotype. Paratypes: 10 ♂, 5 ♀, 9 pupae and 12 larvae (BAH 1), same data as holotype [UCLA].

Aedes (*Howardina*) *albonotatus* of Spielman and Weyer (1965:339-343); in part of Stone, Knight and Starcke (1959:173).

FEMALE. Wing: 3.5 mm. Proboscis: 2.62 mm. Forefemur: 2.36 mm. Abdomen: about 3.25 mm. Essentially similar to *albonotatus* but differing by a slightly larger size and in the following (fig.8). Palpus about 0.16 of proboscis. Hindtarsal segment 3 white scaled in barely more than basal 0.5. Basomedian tergal light scales on abdomen creamy on II-VII. Sternites completely straw yellow up to V, rest with basal straw yellow and apical dark scales.

MALE. Wing: 3.06 mm. Proboscis: 2.45 mm. Forefemur: 2.28 mm. Essentially similar to female in coloration.

MALE GENITALIA (fig.32). As figured; diagnostic characters as in the key. Ninth tergite lobe prominent, with 4 strong setae. Sidepiece length about 3.0 median width; basolateral scales white, remainder dark; tergomesal surface clothed with numerous strong, long setae; distal sternomesal margin with threadlike setae with twisted apices. Clasper broad at base, curved mesad on distal 0.7. Dorsal sclerotization of aedeagus deeply emarginate, producing distinct apical lobes.

PUPA (fig.32). Abdomen: 4.05 mm. Trumpet: 0.54 mm; index about 4.0. Paddle: 0.78 mm. Diagnostic characters as in the key. Chaetotaxy as given below, hairs darkly pigmented. Readily distinguished from *albonotatus* by the shorter paddle, 7-C usually double and 9-VIII at least 5-branched. *Cephalothorax*: Mesonotum moderately pigmented between trumpets; sides and metanotum deeper; trumpets strongly contrasting. Hair 1(1, 1-2), 2(2, 2-4), 3(1), 4(4, 3-6), 5(2, 2-4), 6(1, 1-2), 7(3, 1-3), 8(3, 2-5), 9(1, 1-2), 10(4, 2-5), 11(1), 12(3, 2-5). *Abdomen*: Tergite I uniformly strongly pigmented except for usual membranous areas; other segments imbricate, strongly pigmented, progressively lighter caudad. Segment I: hair 1(3-10 primary branches,

each with many secondary ones), 2(1), 3(1), 4(5, 4-6), 5(5, 3-6), 6(2, 1-3), 7(3, 2-4), 9(1), 10(1, present in many), 11(1, present in a few). Segment II: hair 0(1), 1(6, 4-14), 2(1), 3(1), 4(6, 4-8), 5(1, 1-2), 6(2, 1-3), 7(3, 2-5), 9(1), 10(2, 1-2, present in a few). Segment III: hair 0(1, 1-2), 1(2, 1-4), 2(1), 3(1, 1-2), 4(3, 3-5), 5(1, 1-2), 6(3, 1-4), 7(4, 2-9), 8(3, 2-4), 9(1), 10(2, 2-3), 11(1), 14(1). Segment IV: hair 0(1), 1(1, 1-2), 2(1), 3(3, 2-4), 4(2, 1-3), 5(1, 1-2), 6(2, 1-3), 7(3, 2-4), 8(3, 2-5), 9(1), 10(2, 1-3), 11(1), 12(1, present in one specimen), 14(1). Segment V: hair 0(1, 1-2), 1(2, 1-3), 2(1), 3(1, 1-3), 4(3, 2-5), 5(1, 1-2), 6(2, 1-2), 7(3, 2-4), 8(3, 2-4), 9(1), 10(1, 1-2), 11(1), 14(1). Segment VI: hair 0(1, 1-2), 1(1, 1-3), 2(1), 3(2, 1-2), 4(2, 2-3), 5(1), 6(1), 7(2, 1-3), 8(3, 2-4), 9(1), 10(1, 1-2), 11(1), 14(1, 1-2). Segment VII: hair 0(1, 1-2), 1(1, 1-3), 2(1), 3(2, 1-3), 4(1, 1-2), 5(1), 6(1, 1-2), 7(1), 8(2, 1-3), 9(3, 2-5), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(9, 5-12), 14(1, 1-2). *Paddle*: Uniformly lightly pigmented, midrib slightly darker; dorsal surface with fine denticles; external margin distinctly serrated and faintly emarginate; hair 1-P slender. Male genital lobe extending to 0.65 of paddle, female genital lobe to 0.44.

LARVA (fig.33). Head: 0.92 mm. Siphon: 0.73 mm. Anal Saddle: 0.35 mm. Chaetotaxy as given below, hairs darkly pigmented. Diagnostic characters as given in the key. Readily separated from *albonotatus* by the unequal gills, pecten teeth terminating before middle of siphon and hair 1-S distinctly beyond last pecten tooth. *Head*: Width about 1.06 of length, moderately pigmented, deeper around mouthparts. Mental plate with a strong median tooth and usually 12(11-13) distinct teeth on either side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(9, 7-10), 5(1), 6(2, 1-2), 7(2, 2-3), 8(1), 9(2, 1-3), 10(1), 11(5, 3-6), 12(2, 2-3), 13(1), 14(2, 2-3), 15(2, 2-3). *Antenna*: Length about 0.34 of head; moderately pigmented and without spicules; hair 1-A at about 0.5 from base. *Thorax*: Apices of long hairs attenuate; stellate hairs with a few branches; long and stellate hairs weakly barbed. Prothorax: hair 0(6, 4-6), 1(3, 3-4), 2(1), 3(4, 3-5), 4(3, 2-5), 5(2, 2-3), 6(1), 7(2, 2-3), 8(7, 5-8), 9(2, 1-2), 10(1), 11(2, 1-3), 12(1), 14(20, 17-29). Mesothorax: hair 1(3, 3-4), 2(1), 3(1), 4(1), 5(1, 1-2), 6(5, 4-5), 7(1), 8(6, 5-9), 9(5, 5-8), 10(1), 11(1, 1-2), 12(1), 13(6, 3-7), 14(3, 3-4). Metathorax: hair 1(4, 3-5), 2(1), 3(3, 3-5), 4(3, 2-4), 5(3, 3-5), 6(1), 7(6, 5-7), 8(6, 3-6), 9(5, 4-6), 10(1), 11(1, 1-2), 12(1), 13(4, 4-7). *Abdomen*: Stellate hairs as on thorax. Segment I: hair 1(6, 4-7), 2(7, 6-8), 3(1), 4(6, 4-8), 5(6, 4-9), 6(4, 3-5), 7(1), 9(4, 3-5), 10(1), 11(5, 4-7), 13(4, 2-4). Segment II: hair 0(1), 1(3, 2-4), 2(8, 6-8), 3(1), 4(6, 4-6), 5(5, 3-6), 6(4, 3-5), 7(2, 1-3), 8(2), 9(4, 3-5), 10(1), 11(1, 1-2), 12(1), 13(4, 3-5). Segment III: hair 0(1), 1(3, 2-3), 2(7, 6-8), 3(1), 4(2, 1-3), 5(4, 3-7), 6(3, 2-3), 7(5, 4-7), 8(1), 9(6, 5-7), 10(1, 1-2), 11(1, 1-2), 12(1, 1-2), 13(3, 2-4), 14(1). Segment IV: hair 0(1), 1(2, 2-3), 2(7, 5-8), 3(1), 4(2, 1-3), 5(5, 4-7), 6(3, 2-4), 7(5, 4-6), 8(1, 1-2), 9(6, 6-9), 10(1, 1-2), 11(1, 1-2), 12(1), 13(2, 2-4), 14(1). Segment V: hair 0(1), 1(3, 2-3), 2(8, 6-9), 3(1), 4(2, 2-3), 5(6, 3-9), 6(2, 2-3), 7(5, 4-5), 8(1, 1-2), 9(7, 6-8), 10(1), 11(2, 1-2), 12(1), 13(2, 2-3), 14(1, 1-2). Segment VI: hair 0(1, 1-2), 1(3, 2-5), 2(6, 6-8), 3(1), 4(1), 5(4, 3-5), 6(2, 1-2), 7(4, 3-6), 8(2, 2-3), 9(5, 5-7), 10(1), 11(2, 1-3), 12(1), 13(4, 2-5), 14(2, 2-3). Segment VII: hair 0(1), 1(4, 3-6), 2(7, 6-8), 3(1), 4(1), 5(4, 3-4), 6(3, 2-4), 7(1, 1-2), 8(4, 4-5), 9(3, 3-4), 10(1, 1-2), 11(1, 1-2), 12(1), 13(3, 1-4), 14(3, 2-3). *Segment VIII*: Comb scales in a single row, in the form of a wide chevron, 10-18 in number; individual scale moderate; apex blunt and finely fringed. Hair 0(1), 1(4, 2-5), 2(1), 3(7, 6-8), 4(1), 5(4, 2-4), 14(2, 2-3). *Siphon*: Index about 2.18-2.4; integument imbricate, moderately pigmented, with darker basal ring. Pecten extending to 0.4, usually 10(6-14) teeth, smaller at base, progressively larger distad; individual tooth with long spine and a basal denticle; hair 1-S distinctly distad of last tooth; acus dis-

tinct, free or attached. Hair 1(3, 2-4), 2(1), 3-5 not visible, 6(1), 7(1), 8(2, 2-3), 9(1). *Anal Segment*: Saddle moderately pigmented and imbricate; caudal margin with short spines. Gills short to moderately long, unequal, ventral about 0.5-0.6 of dorsal. Hair 1(2, 1-3), 2(1), 3(4, 4-6), 4a(4, 3-5), 4b(3), 4c(3, 2-4), 4d(3, 3-4), 4e(3, 3-4), 4f(3, 2-4).

EGG. Length about 0.67 mm. Width about 0.14 mm; exochorion transparent, with characteristic circular clear refractive bodies; endochorion dark and with large irregular polygonal sculpturing.

SYSTEMATICS. I have no hesitation in recognizing *bahamensis* as a species distinct from the superficially similar *albonotatus* since the male genitalia are completely different in the 2 forms and the immature stages also appear to be differentiated by constant features mentioned in the diagnosis. In addition to the type series derived from a laboratory colony established from material collected on Grand Bahama Island and described as *albonotatus* by Spielman and Weyer (1965:339-343), I have included under *bahamensis* a single female reared from a treehole on New Providence Island, on which previous records of *albonotatus* from Bahamas were based. Although this specimen agrees well with the type material, the presence of *bahamensis* on New Providence can be confirmed only by additional material, especially males and immature stages.

BIONOMICS. Spielman and Weyer (1965) recorded *bahamensis* (as *albonotatus*) from a wide variety of artificial containers similar to those utilized by *Aedes aegypti* but never in association with the latter. The natural breeding sites of *bahamensis* are probably treeholes, as indicated for the female from New Providence Island, and possibly also rockholes. According to Spielman and Weyer (loc. cit.) females of *bahamensis* are normally autogenous but will occasionally take blood from man or canaries. A laboratory colony was readily established and maintained; eggs produced by autogenous females hatched in tap water after storage for 1-2 weeks at a relative humidity of 76% and a temperature of 76°F.

DISTRIBUTION (fig.3). Bahama Islands. Material examined: 45 specimens; 13 ♂, 8 ♀, 9 pupae, 15 larvae; no individual rearings.

BAHAMA ISLANDS. *Grand Bahama*: village of Hunter, artificial containers, A. Spielman (BAH-1, type series), 11 ♂, 6 ♀, 9 p, 12 L [USNM, UCLA]; 19 July 1964, tire, A. Spielman, 1 ♂ genitalia (GB 71-1), 1 L; 1 Dec 1964, tire. A. Spielman, 1 ♂ (GB 81-52A), 1 ♀ (GB 81-85A) [USNM]. *New Providence*: 1915, treehole, H.G. Dyar, 1 ♀ [USNM].

Busckii Group

FEMALE. *Head*: Narrow decumbent scales pale golden. Palpus completely dark scaled. *Thorax*: Inner dorsocentral line faint, narrow, golden; median prescutellar line narrow, golden; outer dorsocentral line faint, narrow, golden; lateral marginal line narrow, silvery, interrupted at scutal angle and sometimes caudad of it. Acrostichal bristles present on disc. Scutellum with some light scales on lateral lobes. *Ssp* with distinct silvery patch; upper *stp* patch small, separate. *Legs*: Foretarsus completely dark; midtarsus with a few basal white scales on segments 1,2; hindtarsus with short to moderate basal white rings on segments 1-3. *Abdomen*: Basomedian tergal light markings evident from segment V distad.

MALE. Palpus entirely dark. Larger claw of foreleg and midleg with submedian tooth only; smaller claw without either submedian or basal tooth.

MALE GENITALIA. Claspette with a distinct outstanding apical fingerlike cylin-

drical process more than twice as long as wide and bearing a short apical bristle. Clasper about 0.6 of sidepiece; subapical hairs absent. Aedeagus ovate; apex deeply emarginate, with distinct lateral lobes; subequal in length to proctiger.

PUPA. *Cephalothorax*: Hair 5-C double to 4-branched, short but longer than hair 4-C; hair 7-C double to 4-branched; hair 10-C with 2-5 branches. *Abdomen*: All large hairs except 1-II,III, 9-VII,VIII usually single or double; hair 2-II laterad of or in line with hair 3; hair 5-IV,V short, usually not reaching apex of tergite following; hair 9-II-VI usually caudad of level of hair 6; 9-VII longer, stouter and with more branches than hair 6-VII; hair 4-VIII usually single. *Paddle*: Short; apex rounded; marginal spicules distinct.

LARVA. *Head*: 1-C unbranched; 4-C moderately long, multiple; 5-C single, long; 6-C usually double or triple; hairs 11,14-C weakly stellate, 11-C with unequal branches; 15-C usually double, long, exceeding apex of mental plate. *Antenna*: Shaft with a few scattered weak sharp spicules; hair 1-A single. *Thorax*: Hair 13-P absent. Hairs 0,8,14-P, 1,13,14-M, 1,4,5,8,13-T all moderately stellate and moderately pigmented; hairs 1-M,T far mesad of hairs 2,3. *Abdomen*: Integument glabrous; hairs 2 and 9 far removed cephalad but not beyond hair 8. Hairs 1,2,5,9,13-I-VI, 11-I, 7-III-VI all moderately stellate, usually stronger than on thorax; hair 8-VII cephalodorsad of 9-VII. *Segment VIII*: Comb scales varied from 1 more-or-less regular row to 2-4 distinct rows; individual scales moderately long and broad, blunt apically and fringed. *Siphon*: Index less than 3.0; integument without spicules; small separate acus present. Pecten variable, sometimes extending to near apex; teeth always few and widely spaced, short, proximal with basal denticles. *Anal Segment*: Saddle body without distinct spicules; caudal margin with relatively short fringed spines; hair 1-X usually less than 5-branches, near lower end of caudal margin. Ventral brush with 5 pairs of hairs on a moderately sclerotized boss with short median grid bars.

DISCUSSION. Only 1 species is recognized at this time in the Busckii Group although it is evident, as indicated under the species, that there are marked differences among the populations from different islands.

The Busckii Group is immediately separated from all the other groups in the subgenus by the presence of acrostichal bristles on the disc of the mesonotum. The ornamentation of the adults is in general intermediate between the Walkeri Group and the Ioliota-Albonotatus Groups. The larvae of some populations show another primitive feature in the presence of several rows of comb scales, a condition found normally only in the Fulvithorax Group. Since the distributions of these 2 groups are now adjacent and may have overlapped in the past, the comb patch in *busckii* may have been acquired through introgression from the Fulvithorax Group. This does not seem likely because this feature is found only in the northern populations, farthest removed from Fulvithorax Section and because there is no indication of any other introgression between the 2 groups.

The Busckii Group is definitely known only from the Lesser Antilles from Sint Eustatius southward to Grenada (fig.3). This distribution is complementary to the Ioliota and Albonotatus groups except for a possible overlap with the latter in Guadeloupe.

The Busckii Group has the widest range of breeding sites in the subgenus, being found in treeholes, broken bamboo, rockholes, fallen fruits and leaves, as well as in leaf axils of bromeliads and aroids, and in flower bracts of heliconias.

16. *Aedes* (*Howardina*) *busckii* (Coquillett)

Figs. 3, 8, 34, 35

1906. *Stegomyia busckii* Coquillett, 1906:60-61. TYPE: Lectotype ♂, Cacao plantation, San Domingo [Dominica], 28 July 1905, A. Busck [USNM, 9139; selection of Stone and Knight 1956:215].

1919. *Aedes thaxteri* Dyar and Knab, 1919:8-9. TYPE: Holotype ♂, Grand Etang, Grenada, Nov 1912, R. Thaxter [USNM, 21704]. Synonymy with *busckii* by Dyar and Knab (1919:8).

1941. *Aedes tracei* Senevet and Quievreux, 1941:251-258. TYPE: Holotype ♂ (M 2163) with associated pupal skin and genitalia mount, near Piscine Colson, Martinique, 14 Aug 1939, G. Senevet and L. Quievreux [NE; see Belkin 1968]. Synonymy with *busckii* by Belkin, Schick and Heinemann (1965:33).

Aedes (*Howardina*) *busckii* of Bonne and Bonne-Wepster (1925:372-373); Dyar (1928:234-235); Edwards (1932:155); Lane (1939:99); Floch and Abonnenc (1945:14-16, 42, 45, 47); Lane (1953:722-724); Stone, Knight and Starcke (1959:173); Belkin, Schick and Heinemann (1965:17, 33); Porter (1967:38).

Aedes busckii of Dyar and Knab (1906b:189, 192); Howard, Dyar and Knab (1917:860-862); Dyar (1918:73, 80); Senevet (1938:189); van der Kuyp (1954:39, 64, 68, 70, 72, 95, 96); Stone and Knight (1956:215).

Gymnometopa busckii of Coquillett (1906b:25); Theobald (1907:211; 1910:219); Surcouf and Gonzalez-Rincones (1911:212, 213).

Haemagogus busckii of Coquillett (1905:183); Dyar and Knab (1906a:166).

Aedes (*Howardina*) *thaxteri* of Bonne and Bonne-Wepster (1925:276-277); Lane (1939:99).

Aedes (*Soperia*) *tracei* of Lane (1953:703-705); Stone, Knight and Starcke (1959:173); Forattini (1965:460).

FEMALE. Wing: 3.24 mm. Proboscis: 2.19 mm. Forefemur: 2.19 mm. Abdomen: about 3.0 mm. As described for the group and with following additional features. *Head*: Light scales on median stripe pale golden; creamy on sides and venter. *Thorax* (fig. 8): Light patch on anterior promontory silvery. All mesonotal light lines, except lateral marginal, narrow, golden. Antealar area above paratergite with scattered dark scales. Lateral scutellar lobes with a few narrow golden and dark scales. *Legs*: Forefemur and midfemur predominantly dark anteriorly, a few creamy scales at base, posterior surface with a lateral and a median longitudinal creamy line from base to apex on forefemur and midfemur respectively, rest dark; hindfemur predominantly creamy to 0.6, lateral margin and distal area dark. *Haltere*: Stem pale, knob predominantly dark, fringe scales whitish. *Abdomen*: Sternites completely creamy on II-IV; rest of segments with basal creamy and apical dark scales.

MALE. Wing: 2.54 mm. Proboscis: 2.19 mm. Forefemur: 1.84 mm. Essentially similar to female in color.

MALE GENITALIA (fig. 34). As figured; diagnostic features as described for group. Ninth tergite lobe indistinct, with 2, 3 strong bristles. Sidepiece elongate, length about 3.5 median width.

PUPA (fig. 34). Abdomen: 3.35 mm. Trumpet: 0.43 mm; index about 4.0. Paddle: 0.7 mm. Chaetotaxy as given below, hairs moderately pigmented. Diagnostic characters as in the key. *Cephalothorax*: Mesonotum lightly to moderately pigmented between trumpets; lateral areas and metanotum deeper; trumpets strongly contrasting. Hair 1(1), 2(1, 1-2), 3(1), 4(3, 2-4), 5(2, 2-4), 6(1, 1-2), 7(2, 2-4), 8(2, 1-3), 9(1), 10(3, 2-5), 11(1), 12(2, 1-3). *Abdomen*: Tergite I moderately pigmented and imbricate except for usual membranous areas; pigmentation progressively lighter on distal

segments. Segment I: hair 1(9-14 primary branches, each with many secondary ones), 2(1, 1-2), 3(1), 4(4, 3-5), 5(3, 2-6), 6(1, 1-2), 7(2, 1-3), 9(1), 11(1, present in a few). Segment II: hair 0(1), 1(4, 3-7), 2(1, 1-2), 3(1, 1-2), 4(4, 2-5), 5(1, 1-3), 6(1, 1-2), 7(2, 1-3), 8(1, 1-3, present in many), 9(1), 11(1, present in some). Segment III: hair 0(1), 1(2, 1-3), 2(1, 1-3), 3(1, 1-2), 4(3, 2-4), 5(1, 1-4), 6(1, 1-2), 7(3, 2-4), 8(2, 2-3), 9(1), 10(2, 1-2), 11(1), 14(1). Segment IV: hair 0(1), 1(2, 1-3), 2(1), 3(3, 2-4), 4(2, 2-3), 5(2, 1-3), 6(1), 7(2, 2-4), 8(2, 1-3), 9(1), 10(2, 1-3), 11(1), 14(1). Segment V: hair 0(1), 1(1, 1-2), 2(1), 3(2, 1-3), 4(3, 3-5), 5(1, 1-3), 6(1), 7(3, 2-3), 8(2, 1-4), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(1, 1-2), 2(1), 3(2, 1-3), 4(2, 2-3), 5(1, 1-2), 6(1), 7(2, 1-3), 8(2, 1-3), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(2, 1-2), 5(1, 1-2), 6(1, 1-3), 7(1), 8(1, 1-2), 9(5, 3-7), 10(1, 1-2), 11(1), 14(1). Segment VIII: hair 0(1), 4(1, 1-2), 9(7, 5-11), 14(1, 1-2). *Paddle*: Uniformly lightly pigmented, midrib slightly darker; length subequal to or slightly greater than median width; dorsal surface with minute denticles; apex rounded, external margin serrated; hair 1-P slender. Male genital lobe extending to about 0.45 of paddle, female genital lobe to 0.36.

LARVA (fig.35). Head: 0.73 mm. Siphon: 0.59 mm. Anal Saddle: 0.27 mm. Diagnostic characters as in the key. Readily separated from other members of the section by the presence of only 5 pairs of hairs in ventral brush. Chaetotaxy as given below, hairs moderately to darkly pigmented. *Head*: Width about 1.08 of length; integument moderately pigmented, deeper around mouthparts. Mental plate with a strong median tooth and usually 12(10-13) distinct teeth on either side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(11, 10-12), 5(1), 6(2, 2-3), 7(3, 2-5), 8(1), 9(1, 1-3), 10(1), 11(5, 4-10), 12(2, 2-3), 13(1), 14(3, 2-6), 15(2, 2-4). *Antenna*: Length about 0.3 of head; uniformly moderately pigmented, with a few scattered spicules. Hair 1-A at about 0.6 from base. *Thorax*: Apices of long hairs attenuate; stellate hairs with a few to a moderate number of branches; long and stellate hairs weakly barbed. Prothorax: hair 0(7, 6-9), 1(4, 2-5), 2(1), 3(5, 4-8), 4(4, 4-5), 5(2, 2-3), 6(1), 7(2), 8(7, 5-12), 9(2, 1-3), 10(1), 11(3, 2-3), 12(1), 14(20, 19-29). Mesothorax: hair 1(8, 4-12), 2(1), 3(1), 4(1), 5(1), 6(5, 3-5), 7(1), 8(5, 5-7), 9(6, 4-8), 10(1), 11(1, 1-3), 12(1), 13(5, 4-8), 14(7, 3-10). Metathorax: hair 1(6, 3-12), 2(1), 3(2, 1-3), 4(7, 4-10), 5(7, 5-10), 6(1), 7(5, 5-7), 8(5, 4-6), 9(4, 4-6), 10(1), 11(2, 1-3), 12(1), 13(6, 6-13). *Abdomen*: Integument and stellate hairs as on thorax. Segment I: hair 1(7, 4-11), 2(10, 7-13), 3(1), 4(2, 1-3), 5(7, 7-12), 6(5, 3-6), 7(1), 9(4, 3-5), 10(1), 11(9, 7-12), 13(5, 3-6). Segment II: hair 0(1), 1(8, 5-12), 2(12, 7-12), 3(1), 4(2, 1-2), 5(9, 7-11), 6(4, 3-6), 7(4, 2-4), 8(1), 9(5, 4-7), 10(1), 11(1), 12(1), 13(7, 4-12). Segment III: hair 0(1), 1(7, 5-12), 2(10, 8-10), 3(1), 4(1), 5(8, 8-14), 6(2, 2-3), 7(5, 4-7), 8(1), 9(9, 6-10), 10(1), 11(1), 12(1), 13(8, 4-12), 14(1, 1-2). Segment IV: hair 0(1), 1(10, 7-10), 2(10, 7-10), 3(1), 4(1), 5(9, 8-13), 6(2), 7(5, 4-7), 8(1, 1-2), 9(8, 8-10), 10(1), 11(1), 12(1), 13(8, 5-12), 14(1). Segment V: hair 0(1), 1(5, 5-12), 2(10, 7-10), 3(1), 4(1, 1-2), 5(8, 8-12), 6(2), 7(5, 4-8), 8(1), 9(9, 7-10), 10(1), 11(1), 12(1), 13(7, 5-11), 14(1, 1-2). Segment VI: hair 0(1), 1(9, 5-12), 2(8, 5-10), 3(1), 4(1), 5(9, 7-13), 6(2), 7(3, 3-5), 8(2, 1-3), 9(7, 6-10), 10(1), 11(1), 12(1), 13(5, 3-10), 14(2, 1-2). Segment VII: hair 0(1), 1(9, 4-12), 2(7, 5-10), 3(1), 4(1), 5(7, 5-11), 6(3, 3-5), 7(1, 1-2), 8(6, 5-8), 9(3, 2-4), 10(1), 11(1), 12(1), 13(3, 3-7), 14(1). *Segment VIII*: Comb scales varied from a single regular row to a distinct patch of 3,4 rows; individual scale long, blunt apically and fringed. Hair 0(1), 1(10, 6-12), 2(1), 3(7, 6-7), 4(1), 5(6, 3-10), 14(1, 1-2). *Siphon*: Index about 2.2-2.8; integument moderately pigmented, with darker basal ring. Pecten teeth few (6-10), widely spaced; frequently teeth terminate before hair 1-S, occasionally 1,2 teeth extend beyond it; individual tooth

with a long spine and small basal denticle; acus distinct and separate or indistinct. Hair 1(2, 2-4), 2(1), 3-5 not visible, 6(1), 7(1), 8(1), 9(1). *Anal Segment*: Saddle moderately pigmented; caudal margin with moderately large flat spines; individual spine with lateral spinules. Gills short to moderate, broad, unequal, ventral about 0.6 of dorsal. Hair 1(2, 2-4), 2(4, 4-6), 3(1), 4a(4, 3-6), 4b(3, 3-4), 4c(4, 3-4), 4d(4, 4-5), 4e(2, 2-3).

SYSTEMATICS. *A. busckii* in the present interpretation is undoubtedly a complex of closely related and more or less strongly differentiated forms, some of which may be geographically or ecologically isolated species. It is impossible to resolve this complex at this time because of the bewildering array of differentiation and variation in ornamentation of the adults and larval characters which is apparently associated with both isolation on numerous islands and the utilization of a wide variety of breeding sites (see Bionomics below). As in the case of the *Tripteroides caledonicus* complex in the South Pacific (Belkin 1955), the situation may be further complicated through recent mixing of originally isolated insular populations by human transport.

For the present, the currently accepted synonymy of *thaxteri* with *busckii* is retained although there are rather obvious differences in ornamentation of the adults as pointed out in the original description of the former. The synonymy of *tracei*, proposed by Belkin, Schick and Heinemann (1965:33), appears to be well founded since the populations from Martinique are very similar to those from Dominica.

The above diagnosis of the complex is based primarily on topotypic associated material of all stages of *busckii* from Dominica. In the adults, the most striking differences in the various populations are: (1) in the nature of the lateral mesonotal silvery line which may be nearly continuous from the anterior promontory to the wing root or variously broken into segments, (2) in the extent of the basal white ring on hindtarsal segment 3 which varies from less than 0.4 to almost 0.75 of the segment length, and (3) the presence of some white scales on additional tarsal segments. No striking differences have been noted in the pupae but the larvae of different populations show remarkable differentiation from the typical population in: (1) the number and arrangement of scales in the comb from a few scales in a single even row to a large number in a patch of 3 or 4 rows, and (2) the distribution of the pecten which may end before the siphonal tuft or may reach nearly to the tip of the siphon.

The northern populations from Sint Eustatius, St. Kitts, Montserrat and Guadeloupe differ from all the others in the more extensive white ring on hindtarsal segment 3, the larval comb in a large patch and the pecten ending before the siphonal hair tuft. The male genitalia of these populations are also apparently distinct from the others in the large number of setae on the tergal surface of the sidepiece and in a broad aedeagus with distinct apicolateral lobes. Although these populations probably represent a distinct species, I prefer not to name or describe it formally without additional material and a thorough study of the entire complex which is beyond the scope of the present revision.

The *busckii* complex is apparently restricted to the main chain of the Lesser Antilles from Sint Eustatius southward to Grenada. I have seen material only from the above-mentioned islands and from St. Kitts, Montserrat, Guadeloupe, Dominica, Martinique and St. Lucia. No material of the complex was found in a recent survey of Nevis and St. Vincent but it is likely that populations will be found there as well as on the smaller intermediate islands of the chain. The report of *busckii* from Jamaica by Hill and Hill (1948:43) is probably based on an erroneous identification of a member of the Aurites Group and its record from the Dominican Republic is due to the error in labeling the type material San Domingo instead of Dominica (see How-

ard, Dyar and Knab 1917:860).

BIONOMICS. Members of the *busckii* complex have been found breeding in the entire range of habitats utilized by the subgenus, in rockholes, treeholes, broken and cut bamboo, fallen leaves, fruits and pods, in the leaf axils of bromeliads and aroids, and in the flower bracts of heliconias. The immature stages are also commonly found in a variety of artificial containers. One male (FWI 245) from Guadeloupe is reported from a ground pool but this may be a contamination or an error in labeling. Females are frequently taken in biting-landing collections and some were obtained on chicken bait. Apparently some adult populations may reach high levels and become serious pests locally.

DISTRIBUTION (fig.3). Main chain of the Lesser Antilles from Sint Eustatius to Grenada; reported from low (40 ft) to moderate (2600 ft) elevations. Material examined: 1269 specimens; 253 ♂, 273 ♀, 290 pupae, 453 larvae; 175 individual rearings (19 pupal, 131 larval, 25 incomplete).

DOMINICA. *St. Andrew*: Calibishie, 23 June 1965, colocasia leaf axil, R. Martinez and A. Guerra, 1 p, 2 l (DOM 137), 2 lp♂ (138-10,11), 1 lp♀ (138-13), 1 P (DOM 138) [UCLA]. *St. David*: Castle Bruce, 19 Apr 1959, bamboo, R.H. Darsie, 1 lp♂ (76-14), 2 p♂ (76-15A,16), 1 ♂ (76-10), 1 lp♀ (76-6), 4 ♀ (76-2,4A,7,11), 1 lP, 1 P [USNM]. Grand Fond, elev. 300 ft, 18 June 1965, biting collection, R. Martinez and A. Guerra, 1 ♀ (DOM 116) [UCLA]. Terre Ferme, elev. 1800 ft, 22 June 1965, heliconia bract, R. Martinez and A. Guerra (DOM 131), 1 lp♂ (131-12), 1 lp♀ (131-11), 6 ♂, 12 p, 2 L [UCLA]. *St. George*: L'Etang, elev. 2600 ft, 8 June 1965, bromeliads, T.H.G. Aitken, R. Martinez and A. Guerra, 1 p (DOM 53) [UCLA]. Trafalgar Falls, elev. 1700 ft, 9 June 1965, biting collection, R. Martinez and A. Guerra, 4 ♀ (DOM 58); heliconia bract (DOM 59), 2 lp♀ (59-10,11), 1 P, 1 p [UCLA]. *St. Joseph*: Batati Estate, elev. 40 ft, 14 June 1965, treehole, R. Martinez and A. Guerra (DOM 82), 1 lp♀ (82-20) [UCLA]. Clarke Hall Estate, 12 Nov 1964, P.J. Spangler, 1 ♀; 11 Mar 1964, D.F. Bray, 2 ♀; 21-31 Jan 1965, W.W. Wirth, 3 ♀; 24 Jan 1965, W.W. Wirth, 2 ♀; 3 May 1966, R.J. Gagne, 1 ♀; 11 May 1966, G. Steyskal, 1 ♀; 19 May 1966, G. Steyskal, 1 ♀; 24 May 1966, G. Steyskal, 3 ♀; 1 June 1966, G. Steyskal, 1 ♀; 3 June 1966, G. Steyskal, 1 ♀; 10 June 1966, G. Steyskal, 6 ♀; 11 June 1966, G. Steyskal, 2 ♀; 12 June 1966, G. Steyskal, 1 ♀; 10 Oct 1966, A.B. Gurney, 1 ♀ [USNM]. *St. John*: Milton Estate, elev. 1000 ft, 24 June 1965, heliconia bract, A. Guerra (DOM 159), 2 lp♂ (159-10,13), 1 p♂ (159-101), 2 P, 4 p, 14 L [UCLA]. *St. Luke*: Point Michele, Champigny Estate, elev. 600-700 ft, 6 June 1965, treehole, T.H.G. Aitken, R. Martinez and A. Guerra, 2 lp♂ (15-20,22), 1 lp♀ (15-23), 1 P, 1 p, 1 l (DOM 15), 1 lp♂ (19-10), 4 ♂, 8 p, 7 L (DOM 19), 4 L (DOM 20), fallen leaf, 1 lp♀ (17-10), 2 p, 6 L, 2 l (DOM 17), steel drum, 3 ♂, 1 ♀ (DOM 21), heliconia bract, 4 ♂, 1 ♀ (DOM 23) [UCLA]. *St. Mark*: Tete Morne, elev. 1400 ft, 10 June 1965, heliconia bract, R. Martinez and A. Guerra (DOM 68), 2 lp♂ (68-12,14), 2 lp♀ (68-11,13), 4 ♂, 8 p, 4 L [UCLA]. *St. Paul*: Antrim Valley, 7 June 1965, treehole, R. Martinez and A. Guerra, 4 ♀, 4 p, 4 L (DOM 35) [UCLA]. Mount Joy, elev. 1000 ft, 7 June 1965, treehole, R. Martinez and A. Guerra (DOM 41), 1 lp♂ (41-15), 2 lp♀ (41-10,11), 1 P, 11 L [UCLA]. Pont Casse, 23 Nov 1964, P.J. Spangler, 1 ♂ [USNM]. *Parish not specified*: July 1905, in sugar boiler full of vegetation, 1 ♂, 1 ♀ (78), type series [USNM no. 9139].

GRENADA. *St. Andrew*: Balthazar Estate, elev. 450 ft, 15 Oct 1963, bamboo, R. Martinez, 1 lp♂ (43-125), 1 lp♂ (44-136), 1 lp♀ (44-131) [UCLA]. Mt. St. Catherine, elev. 2000 ft, 25 Oct 1963, bamboo, R. Martinez, 2 L (GR 82), heliconia bract, 2 ♀ (GR 85) [UCLA]. *St. David*: Minorca Estate, elev. 700 ft, 24 Oct 1963, colocasia leaf axil, R. Martinez, 3 L (GR 76); 1 Nov 1963, fallen cacao pod, R. Martinez (GR 111), 1 lp♂ (111-18) [UCLA]. *St. George*: Annandale, elev. 700 ft, 25 Aug 1929, leaf axil, F.M. Root, 18 ♂, 24 ♀ (LAR 40), 5 ♀ (LAR 40A); 28 Oct 1963, bamboo, R. Martinez, 1 L (GR 95), rockhole (GR 96), 1 lp (96-156) [UCLA]. Grand Etang, 2 July 1929, F.M. Root, 20 ♂, 40 ♀ (GRR 11); 26 Aug 1929, leaf axil, F.M. Root, 21 ♂, 4 ♀ (LAR 42); 17 Oct 1963, heliconia bract, R. Martinez (GR 54), 1 lp♀ (54-132), bamboo (GR 59), 1 lp♂ (59-133), fallen palm leaf, 9 ♂, 3 ♀ (GR 60), heliconia bract (GR 61), 1 lp♂ (61-127), 1 lp♀ (61-139); 18 Oct 1963, biting collection, R. Martinez, 1 ♀ (GR 62); 23 Oct 1963, heliconia bract, R. Martinez (GR 67), 1 lp♂ (67-140), 1 ♂ [UCLA]. *St. Mark*: Concord, F.M. Root, 27 ♂, 15 ♀ (GRR 80) [UCLA].

Parish not specified: F.M. Root, 11 ♂, 29 ♀ (GRR 40) [UCLA].

GUADELOUPE. *Basse-Terre*: Capesterre, 76 L, Matouba, 72 L; Petit-Bourg, 17 L; Pointe-Noire, 12 L (Floch and Abonnenc 1945:16). Route de Traversee, km 4-6, elev. 200 ft, 18 Sept 1965, ground pool, P. Fauran, 1 ♂ (FWI-245) [UCLA]. St. Claude, Bains Jaunes, elev. 900 ft, 31 Mar 1965, heliconia bract, P. Fauran, 2 lp♂ (211-12,13), 5 lp♀ (211-10,11,15-17), 2 IP (211-14,18), 4 lp♂ (212-11,13,15,16), 2 lp♀ (212-10,14), 1 IP (212-12) [UCLA]. Soufriere, 111 L; Trois-Rivieres, 51 L (Floch and Abonnenc 1945:16). Vernou, elev. 300 ft, 20 July 1964, treehole, P. Fauran (FWI 182), 4 lp♂ (182-101,102,105,107), 6 lp♀ (182-103,106,108,110,112,113), 1 IP (182-111), 2 L [UCLA]. Locality not specified, elev. 3000 ft, July 1905, wild canna, A. Busck, 1 lp♂ (80-10), 2 ♀ (80-3,7), 3 ♂, 4 ♀ [USNM].

MARTINIQUE. Fort de France, 1929, bamboo, F.M. Root, 2 ♂ (LAR 23), bromeliads, 1 ♀ (LAR 28A) [UCLA]; Route de la Trace, elev. 680 ft, 16 July 1965, heliconia bract, P. Fauran (FWI-M2), 2 lp♂ (M2-10,11), 1 lp♀ (M2-14), 3 p♂ (M2-15,101,102), 2 p♀ (M2-12,100), 1 IP (M2-13), 3 p, 1 l [UCLA]. Mt. Pelee, July 1905, A. Busck, 2 ♀ [USNM]. Piscine Colson, 14 Aug 1939 (Senevet and Quievreux 1941:263).

MONTSERRAT. *St. Antony*: Chance Mountain, elev. 2600 ft, 5 Oct 1966, treehole, T.H.G. Aitken, R. Martinez and A. Guerra, 2 P, 10 L (MNT 25), 2 lp♂ (28-10,11), 1 lp♀ (28-13), 1 p♂ (28-100), 2 IP (28-12,14), 19 L (MNT 28), 1 lp♂ (29-10), 2 lp♀ (29-11,12), 3 L (MNT 29), heliconia bract (MNT 27), 4 lp♂ (27-12,13,15,16), 2 lp♀ (27-10,14), 1 p♂ (27-100), 1 IP (27-17), 5 L [UCLA]. Parsons Estate, elev. 500 ft, 13 Oct 1966, tin can, R. Martinez and A. Guerra (MNT 72), 1 IP (72-10), 9 L [UCLA]. Soufriere, elev. 1000 ft, 12 Oct 1966, bamboo, R. Martinez and A. Guerra, 1 IP (66-10), 1 p, 5 L (MNT 66), 5 L (MNT 67) [UCLA]; Lower Gages, 1250 ft, 6 Oct 1966, treehole, R. Martinez and A. Guerra, 8 L (MNT 36) [UCLA]; Upper Gages, 1750 ft, 6 Oct 1966, heliconia bract, T.H.G. Aitken, R. Martinez and A. Guerra (MNT 38), 1 lp♂ (38-10), 1 p♂ (38-100), 1 p♀ (38-101), 5 L [UCLA]. Waterworks Estate, elev. 550 ft, 18 Oct 1966, treehole, R. Martinez and A. Guerra (MNT 118), 1 p♀ (118-100), 1 IP (118-20) [UCLA]. *St. Peters*: Plymouth, Belham Bridge, elev. 250 ft, 4 Oct 1966, tin can, T.H.G. Aitken, R. Martinez and A. Guerra (MNT 20), 2 lp♂ (20-11,12), 1 lp♀ (20-10), 1 p♂ (20-100), 1 p♀ (20-101), treehole (MNT 22), 1 lp♂ (22-14), 3 lp♀ (22-10-12), 1 IP (22-13), 9 ♂, 3 ♀, 12 p [UCLA].

SINT EUSTATIUS. 7 Oct 1947, E. van der Kuyp, 2 ♂, 1 ♀ [USNM].

ST. KITTS. *Christ Church*: Old Road Town, elev. 1200 ft, 5 Sept 1966, heliconia bract, A. Guerra, 1 ♂, 2 ♀; 5 Sept 1966, R. Martinez and A. Guerra, 1 p♀ (93-101), 2 ♂, 1 ♀ (KIT 93), 1 ♂, 4 ♀ (KIT 94) [UCLA]. *St. John*: Dieppe Bay Town, slopes of Mount Misery, elev. 2500 ft, 17 Aug 1966, treehole, T.H.G. Aitken, R. Martinez and A. Guerra (KIT 25), 1 lp♀ (25-10), 1 IP (25-11), 6 ♂, 2 ♀, 8 p, 1 L [UCLA].

ST. LUCIA. *Anse la Raye*: Elev. 300 ft, 15 July 1964, treehole, R. Martinez and A. Guerra, 1 L (LU 30); 30 July 1964, fallen fruit, A. Guerra, 1 lp♀ (125-20), 1 p♀ (125-100), 1 lp♂ (126-20), 4 L (LU 126), treehole (LU 128), 7 lp♀ (128-10-16), 1 IP (128-17), 26 ♂, 10 ♀, 19 P, 11 L [UCLA]; Derriere Dos, 31 July 1964, fallen cacao pod, A. Guerra (LU 131), 1 lp♂ (131-24), 5 lp♀ (131-20-23,25), 4 ♂, 12 ♀, 8 p [UCLA]. Barre de L'Isle, elev. 800-900 ft, 14 July 1964, treehole, T.H.G. Aitken, R. Martinez and A. Guerra, 3 lp♂ (14-14-16), 6 lp♀ (14-10-13,18,19), 8 p, 7 L, 3 l (LU 14), 2 ♀ (LU 16), 1 ♀ (LU 18); 1 Aug 1964, treehole, R. Martinez and A. Guerra, 3 L (LU 143); 6 Aug 1964, bamboo, R. Martinez and A. Guerra, 14 L (LU 159), 20 L (LU 160), 3 lp♂ (161-12,13,14), 1 IP (161-13), 3 p (LU 161) [UCLA]. *Castries*: Bise Quarry, elev. 250 ft, 17 July 1964, treehole, R. Martinez and A. Guerra (LU 46), 3 lp♀ (46-20,22,23), 2 IP (46-21,24), 3 L, 1 l [UCLA]. Cul de Sac Estate, 30 July 1964, chicken bait, R. Martinez and A. Guerra, 2 ♀ (LU 129) [UCLA]. Delgos, elev. 750 ft, 14 July 1964, bamboo, T.H.G. Aitken, R. Martinez and A. Guerra, 3 lp♂ (10-11,13,15), 2 lp♀ (10-12,14), 1 IP (10-16), 1 P, 7 L (LU 10), 3 lp♀ (11-13-15), 1 p♀ (11-101), 3 IP (11-10,12,18), 1 p, 7 L (LU 11), 3 lp♀ (12-10-12), 3 L (LU 12), treehole (LU 13), 2 L, 1 l [UCLA]. Grande Anse, elev. 175 ft, 20 July 1964, heliconia bract, R. Martinez and A. Guerra, 1 L (LU 62), bamboo (LU 63), 1 lp♂ (63-11), 4 lp♀ (63-10,12-14), 1 p♂ (63-101), 2 L, 1 l [UCLA]. La Croix Junction near Poix Bouche, elev. 500 ft, 20 July 1964, treehole, R. Martinez and A. Guerra (LU 59), 1 lp♂ (59-10), 6 L [UCLA]. Marquis Estate, elev. 200 ft, 20 July 1964, fallen cacao pod, R. Martinez and A. Guerra, 1 ♂, 1 ♀, 1 p, 3 L (LU 60), fallen cocoanut (LU 61), 2 lp♀ (61-10,13),

1 p♀ (61-11), 16 L [UCLA]. Piton Flor, elev. 1875 ft, 4 Aug 1964, bamboo, R. Martinez and A. Guerra (LU 146), 1 lp♂ (146-10), 1 L [UCLA]. Union Agricultural Station, elev. 200 ft, 16 July 1964, bamboo, R. Martinez and A. Guerra (LU 42), 1 lp♀ (42-10), 3 lP (42-11,13,14), 10 L [UCLA]. Waterworks Road, 20 July 1964, bromeliads, R. Martinez and A. Guerra (LU 67), 1 p♀ (67-100) [UCLA]. *Micoud*: Mahaut, elev. 700 ft, 27 July 1964, heliconia bract, A. Guerra (LU 101), 2 lp♂ (101-14,15), 2 lp♀ (101-12,13), 1 lP (101-11), 9 L [UCLA]. Mon Repos, elev. 300 ft, 28 July 1964, bromeliads, A. Guerra (LU 104), 1 lp♂ (104-11), 6 L [UCLA]. *Soufriere*: Soufriere, elev. 220-500 ft, 20 July 1964, heliconia bract, R. Martinez and A. Guerra, 2 L (LU 78), bamboo (LU 80), 4 lp♂ (80-10-13), 2 lp♀ (80-14,15), 10 L; 22 July 1964, fallen cacao pod, R. Martinez and A. Guerra (LU 83), 1 lp♀ (83-11), 3 L [UCLA].

SEXLINEATUS SECTION

FEMALES. Medium sized to rather large species, wing 2.7-5.0 mm. *Head*: Submedian and lateral dark patches broad, distinct. Erect scales restricted to occiput. Torus dark brown to almost black, with light scales restricted usually to mesal surface. Palpus with or without apical light scales. *Thorax*: Mesonotum always with distinct linear light pattern, light lines of same color throughout, white, creamy or golden (except in *ecuadoriensis*). Acrostichal line not developed but a small patch of light scales present at anterior promontory; inner and outer dorsocentral lines usually long, both reaching scutellum; lateral marginal line usually continuous (broken in Whitmorei Group); median prescutellar line not developed. Paratergite with scales. Acrostichal bristles absent on disc. Pleural scales silvery, white or creamy; *ppn* and *ssp* with scales; *psp* usually with scales (usually absent in Allotecnnon Group); *mep* with separate upper and lower patches. *Legs*: Midfemur and hindfemur sometimes with distal white spots on anterior surface. All tibiae usually completely dark (except Sexlineatus and Whitmorei Groups). Tarsal light markings not restricted to segment 1. *Wing*: Light scales present on remigium in Aurivittatus Group, absent in others. *Abdomen*: Sternites II-IV with dark scales distally.

MALES. Larger claw of foreleg and midleg with submedian tooth only.

MALE GENITALIA. Lobes of tergite IX either poorly defined or distinct, bearing a few to many strong to moderate setae. Sidepieces separated from each other at base by a distance less than diameter of aedeagus at that level (greater in Whitmorei Group); tergomesal and/or sternomesal margins with lobes only in Whitmorei Group. Claspette completely absent in Whitmorei Group, represented in other groups by sternal basomesal lobe not connected across midline and bearing 1 apical seta.

PUPAE. *Cephalothorax*: Hair 5-C longer than distance between its base and that of trumpet, strong and always double, at least 2.0 of hair 4-C. *Abdomen*: Hair 5-IV, V strong, usually double, extending distinctly beyond apex of tergite following; 2-IV-VI usually within basal 0.6 of its tergite; hair 9-III-VI distinctly cephalo-laterad of hair 6; 9-VII moderate to strongly developed, removed considerable distance cephalad of hair 6.

LARVAE. Stellate hairs always strongly developed. *Antenna*: Short to moderate; shaft with scattered spicules; hair 1-A usually 2,3-branched. *Thorax*: Integument with or without spicules. Tubercles of hairs 5-7-P distinctly joined; hair 9-P with more than 4 branches and faintly stellate; 13-P present, distinctly stellate. *Abdomen*: Integumentary spiculation strong or weak, sometimes confined to dorsal or ventral surface, spicules usually hairlike (spinelike in Allotecnnon Group). Hairs 1,2,5,11,13-I, 1,2,5,7,9 (and usually 13)-II-VII stellate; hair 8-VII cephalodorsad or caudodorsad

of 9-VII. *Segment VIII*: Hair 1,5-VIII usually stellate. Comb scales in a single row; individual scales long, pointed apically. *Siphon*: Index 2.0-4.3; integument smooth, imbricate or spiculate. Acus distinct, separate or attached. Pecten teeth with basal denticles. *Anal Segment*: Saddle with distinct marginal spicules. Hair 1-X moderate, with few branches; 3-X single or double; 2-X multiple. Ventral brush with 5 or 6 pairs of hairs arising from a boss with distinct grid bars.

DISCUSSION. The ornamentation pattern of the adults of the *Sexlineatus* Section is superficially so similar in most species that few specimens have been correctly identified in the past and many distinct species were not recognized until in the present study correlated differences were found in the immature stages. On the whole, the section is a homogeneous one and strongly differentiated from the other 2 sections in all stages as indicated in the keys and diagnosis. As far as is known, members of this section breed only in bromeliad axils.

The *Sexlineatus* Section is primarily associated with the great cordilleras of Central America and western South America. Apparently only the monotypic *Sexlineatus* Group and the *Whitmorei* Group penetrate eastward into the lowlands of the Orinoco and the smaller northern South American drainages and no species extends even to the Guianas. There are only small extensions from the Andes down into moderate elevations near the headwaters of the Orinoco, Amazon and La Plata basins (fig.1).

Only 2 of the 6 groups recognized here for the 19 species are strongly differentiated: (1) the *Quadrivittatus* Group which is confined to Middle America and appears to have retained the most significant primitive features in the section, and (2) the *Whitmorei* Group which is known in Colombia, Venezuela and Bolivia but undoubtedly also occurs in Ecuador and Peru; this is the most derived group in the section. The remaining 4 groups show considerable overlap in many characters although the *Sexlineatus* and *Allotecnion* Groups each have a characteristic facies in the adult and larval stages. The *Eleanorae* Group in many respects appears intermediate between the *Quadrivittatus* and the *Allotecnion* Groups. The separation of the *Aurivittatus* Group from the *Eleanorae* Group is based only on the presence of light scales on the remigium of the wing of the former; when the immature stages are known the 2 taxonomic groups may have to be merged.

Two of the groups, *Quadrivittatus* and *Allotecnion*, are confined to Middle America where they are sympatric and extend northward to southern and central Mexico. The monotypic *Sexlineatus* Group overlaps with the above throughout their range in Middle America but is apparently not completely sympatric with them; it further extends along the Pacific coast to the Gulf of Guayaquil and along the southern Caribbean shores to Trinidad; it is the only species of the section to be found near sea level. The *Whitmorei*, *Eleanorae* and *Aurivittatus* Groups are confined to South America. The dominant *Eleanorae* Group is primarily Andean and has a wide distribution from western Venezuela and Colombia down to Bolivia, with slight intrusions into the upper Orinoco and Amazon basins. The *Aurivittatus* Group is known only from the upper drainages of the Amazon and La Plata in Bolivia and northern Argentina respectively. The *Whitmorei* Group has been found in Colombia, Venezuela and Bolivia and has small intrusions into the upper Orinoco, Amazon and La Plata drainages.

Both in Middle and South American groups, some members of a given group seem to occur sympatrically, others are allopatric and still others appear to be ecologically isolated (in the *Eleanorae* Group) although broadly sympatric.

KEYS TO GROUPS AND SPECIES

ADULTS

- 1. Midfemur without any indication of a white or silvery spot or streak on anterior surface above ventral light line (Quadrivittatus Group) 2
- Midfemur with a more or less distinct white or silvery spot or streak on anterior surface above ventral light line 4

Quadrivittatus Group

- 2(1). Outer dorsocentral line not reaching lateral marginal line anteriorly 19. *brevis*; 20. *spinosus*
- Outer dorsocentral line connected to lateral marginal line anteriorly 3
- 3(2). *Ppn* scales predominantly narrow and yellowish; *ssp* scales in a restricted linear patch not connected to *ppn* patch; first flagellar segment with dark scales 17. *quadrivittatus*
- Ppn* scales predominantly broad and white; *ssp* scales extending toward *ppn* patch, the 2 patches usually connected; first flagellar segment with white scales 18. *lorraineae*
- 4(1). Antealar area (above paratergite) with numerous dark bronzy scales below narrow supraalar golden line (Sexlineatus and Whitmorei Groups) 5
- Antealar area with whitish, yellowish or golden scales only, so that lateral marginal and supraalar lines are united 7

Sexlineatus Group

- 5(4). Outer dorsocentral line reaching anterior border of mesonotum; torus with small mesal patch of white or whitish scales. 21. *sexlineatus*
- Outer dorsocentral line not reaching anterior border of mesonotum, directed outward toward lateral mesonotal line in fossa; torus with a broad ring of white or silvery scales interrupted only dorsally (Whitmorei Group) 6

Whitmorei Group

- 6(5). Hindtarsal white rings on segments 1,2 and 3; anterior end of outer dorsocentral line with a patch of broad silvery scales 22. *whitmorei*
- Hindtarsal white rings on segments 1 and 2 only; anterior end of outer dorsocentral line without patch of broad silvery scales 23. *pseudodominicii*
- 7(4). Base of vein R (remigium) with white or whitish scales 8
- Base of vein R with dark scales as elsewhere. 10

Aurivittatus Group

- 8(7). Hindtarsal white ring on segment 1 only; haltere knob with white scales only 35. *vanemdeni*
- Hindtarsal white rings on segments 1,2 and 3; haltere knob with both dark and light scales 9

- 9(8). Outer dorsocentral line reaching anterior border of mesonotum; lateral marginal line poorly developed in front of scutal angle, without broadened scales 33. *aurivittatus*
 Outer dorsocentral line not reaching anterior border of mesonotum; lateral marginal line strongly developed in front of scutal angle, with broadened scales 34. *martinezi*

Eleanorae Group

- 10(8). Hindtarsus with basal white rings on segments 1 and 3 only. . 27. *eleanorae*
 Hindtarsus with basal white rings on segments 1,2, 1-3 or 1-4 11
- 11(10). Hindtarsus with basal white rings on segments 1-4 12
 Hindtarsus with basal white rings on segments 1,2 or 1-3 only. 13
- 12(11). Inner dorsocentral line white, usually very narrow; *ppn* with narrow curved light scales in upper part and broad flat white scales in lower; *ssp* scale patch extended upward toward *ppn* broad scales; hindtarsal markings broad, on segment 4 about 0.5 of segment length . . . 31. *ecuadoriensis*
 Inner dorsocentral line yellowish, usually broadened anteriorly; *ppn* predominantly with moderately broad, curved, light scales throughout; *ssp* scale patch entirely linear, not extended to *ppn* scales; hindtarsal markings narrower, on segment 4 usually less than 0.2 of segment length
 32. *brevivittatus*
- 13(11). Hindfemur without silvery spot on the anterior surface; *ssp* scale patch narrow, linear and not extended toward *apn* or *ppn* scale patches. . . . 14
 Hindfemur with a very distinct silvery spot on dark portion of anterior surface not connected to basal ventral light streak; *ssp* scale patch short and broad and extended toward *apn* and *ppn* scale patches (Allotecnnon Group)
 16
- 14(13). Midfemoral light patch or spot at about 0.5. 30. *osornoi*
 Midfemoral light patch at about 0.67 or distad 15
- 15(14). Outer dorsocentral line strongly broadened anteriorly and joining lateral mesonotal line 28. *marinkellei*
 Outer dorsocentral line not strongly broadened anteriorly and not joining lateral mesonotal line 29. *leei*

Allotecnnon Group

- 16(13). Hindtarsus with basal white rings on segments 1 and 2 only.
 26. *guatemala*
 Hindtarsus with basal white rings on segments 1-3. 17
- 17(16). *Ppn* with pure white broad flat scales except for narrow upper border of yellowish curved moderately broad scales; *psp* scales usually present. . . .
 25. *guerrero*
Ppn predominantly with yellowish, narrow to moderately broad, curved

scales throughout except at lower posterior angle where a few broad white flat scales may be present; *psp* scales absent. 24. *allotecnnon*

MALE GENITALIA

(18. *lorraineae*; 25 *guerrero*; 26 *guatemala*; 28. *marinkellei*; and 34. *martinezi* unknown; 35. *vanemdeni* not included)

- 1. Claspette completely absent. 2
Claspette represented by a small sternomesal lobe bearing a differentiated apical seta 3

- 2(1). Tergomesal and sternomesal margins of sidepiece with row of flattened foliiform setae 22. *whitmorei*
Tergomesal and sternomesal margins of sidepiece with simple bristles 23. *pseudodominicii*

- 3(1). Apex of aedeagus in dorsal aspect uniformly sclerotized, smoothly rounded, without indication of apical lateral lobes or apical horns 21. *sexlineatus*
Apex of aedeagus deeply emarginate and with distinct long apical horns; or dorsal sclerotization more or less emarginate apically, producing lateral sclerotized lobes 4

- 4(3). Apex of aedeagus with slender horns, bent dorsad . 19. *brevis*; 20. *spinosus*
Dorsal sclerotization of aedeagus more or less deeply emarginate, producing lateral sclerotized lobes 5

- 5(4). Spiniform of clasper short and thick, usually less than 0.25 of clasper length 6
Spiniform of clasper long and slender, usually at least 0.33 of clasper length 9

- 6(5). Aedeagus longer than proctiger 29. *leei*
Aedeagus shorter than or subequal to proctiger 7

- 7(6). Inner setae of ninth tergite lobe very markedly flattened, almost leaflike. 31. *ecuadoriensis*
Inner setae of ninth tergite lobe thickened but not markedly flattened . . 8

- 8(7). Dorsal sclerotization of aedeagus deeply emarginate, lateral apical lobes conspicuous 17. *quadrivittatus*
Dorsal sclerotization of aedeagus shallowly emarginate, lateral apical lobes inconspicuous 24. *allotecnnon*

- 9(5). Spiniform of clasper about 0.5 of clasper length 27. *eleanorae*; 33. *aurivittatus*
Spiniform of clasper less than 0.4 of clasper length 10

- 10(9). Dorsal sclerotization of aedeagus deeply emarginate, lateral apical lobes conspicuous 32. *brevivittatus*

Dorsal sclerotization of aedeagus shallowly emarginate, lateral lobes inconspicuous 30. *osornoi*

PUPAE

(23. *pseudodominicii*; 26. *guatemala*; 31. *ecuadoriensis*; 32. *brevivittatus*; 33. *aurivittatus*; 34. *martinezi* and 35. *vanemdeni* unknown; 18. *lorraineae* and 25. *guerrero* not included)

- 1. Trumpet short and broad, index about 3.0 22. *whitmorei*
Trumpet long and narrow, index over 5.0 2
- 2(1). Hairs 10,11,12-C all single 3
At least one of these hairs branched, usually 10-C. 4
- 3(2). Hair 8-VII on dorsal surface 29. *leei*
Hair 8-VII on ventral surface 28. *marinkellei*
- 4(2). Hair 8-VII on dorsal surface, strongly developed 27. *eleanorae*
Hair 8-VII on ventral surface, weak 5
- 5(4). Paddle deeply emarginate at hair 1 19. *brevis*
Paddle rounded or produced at hair 1 6
- 6(5). Hair 5-IV-V moderate, not exceeding apex of second tergite following . . 7
Hair 5-IV-V very long, exceeding apex of second tergite following . . . 8
- 7(6). Hair 9-VII weak and short, barely reaching lateral angle of tergite . . .
. 30. *osornoi*
Hair 9-VII stronger and longer, extending beyond lateral angle of tergite .
. 21. *sexlineatus*
- 8(6). Hair 1-II usually double or triple; 9-VIII with 3,4 branches
. 24. *allotecnon*
Hair 1-II usually at least 5-branched; 9-VIII with at least 4 branches . . 9
- 9(8). Hair 9-VIII usually at least 8-branched; 9-VII at least 4-branched
. 17. *quadrivittatus*
Hair 9-VIII usually 6-branched; 9-VII double 20. *spinosus*

LARVAE

(23. *pseudodominicii*; 26 *guatemala*; 31. *ecuadoriensis*;
32. *brevivittatus*; 33. *aurivittatus*; 34. *martinezi* and
35. *vanemdeni* unknown)

- 1. Ventral brush with 6 pairs of hairs (Quadrivittatus Group) 2
Ventral brush with 5 pairs of hairs 5

Quadrivittatus Group

- 2(1). Siphon without spicules visible at 100X; hair 12-C double 3

- Siphon distinctly spiculate at 100X; hair 12-C stellate, with many branches
..... 4
- 3(2). Hair 5-C usually with 5 branches 17. *quadrivittatus*
Hair 5-C usually with 3,4 branches 18. *lorraineae*
- 4(2). Hair 5-C usually with more than 10 branches (11-22); siphon index about
2.0 19. *brevis*
Hair 5-C usually 5-branched (4-7); siphon index about 3.0 . . . 20. *spinosus*

Whitmorei Group

- 5(1). Siphon with distinct spicules visible at 100X 22. *whitmorei*
Siphon without spicules visible at 100X 6
- 6(5). Hair 15-C usually triple, very short, at most reaching level of base of mental
plate. 7
Hair 15-C usually single or double, moderate in length, reaching level of mid-
dle of mental plate (Eleanorae Group). 9

Sexlineatus Group

- 7(6). Thoracic and abdominal integument with dense vestiture of hairlike spicules
..... 21. *sexlineatus*
Thoracic integument glabrous at 100X, abdominal with restricted dorsal and
ventral patch of small spinelike spicules (Allotecnon Group) 8

Allotecnon Group

- 8(7). Anal saddle with distinct large caudal marginal spicules ventrad of hair 1-X.
..... 24. *allotecnon*
Anal saddle without any caudal marginal spicules ventrad of hair 1-X . . .
..... 25. *guerrero*

Eleanorae Group

- 9(6). Siphonal hair 1-S within last pecten tooth; hair 5-C with more than 5
branches 27. *eleanorae*
Siphonal hair 1-S distad of last pecten tooth; hair 5-C single or double . 10
- 10(9). Hair 3-X single 30. *osornoi*
Hair 3-X double 11
- 11(10). Siphonal hair 1-S usually single and strongly barbed, rarely double; stellate
hairs all shorter than saddle length, abdominal hairs 1 and 2 usually with
about 10-15 branches 28. *marinkellei*
Siphonal hair 1-S usually triple or double; many stellate hairs distinctly long-
er than saddle, abdominal hairs 1 and 2 usually with 20 or more branches
..... 29. *leei*

Quadrivittatus Group

FEMALES. *Head*: Median light line on vertex with narrow scales. Proboscis distinctly longer than forefemur. Torus with a restricted mesal scale patch. *Thorax*: Mesonotal light lines usually creamy to golden; inner dorsocentral line complete; outer dorsocentral line either complete or incomplete, not reaching anterior margin; lateral marginal line continuous; scales on anterior promontory golden. Antealar area above paratergite with golden scales. Paratergite with a moderate scale patch extending entire sclerite length. Upper *ppn* entirely covered with light scales; upper *stp* patch quadrate. *Legs*: Distal white spot on anterior surface of midfemur and hindfemur absent. Tibiae completely dark. *Wing*: Veins entirely dark scaled. *Abdomen*: Basomedian tergal light markings absent.

MALES. Palpus entirely dark scaled.

MALE GENITALIA. Lobe of tergite IX prominent to indistinct, bearing few (3-5) strong or many (8-10) moderate bristles. Sidepieces separated at base by a distance less than width of aedeagus; without any indication of lobes on tergomesal or sternomesal margins. Claspette represented by a conical tubercle. Aedeagus shorter than proctiger; apex moderate to deeply emarginate, producing lateral lobes or horns.

PUPAE. *Cephalothorax*: Trumpet moderate, index about 5.5-6.0, not expanded apically; hair 10-C at least 5-branched; 12-C single, rarely double. *Abdomen*: Hair 5-IV-V moderate to long, usually exceeding apex of second tergite following (except in *brevis*); hair 9-VII distinctly stronger than hair 6, exceeding lateral angle of tergite. *Paddle*: Moderate to long; apex usually produced (emarginate in *brevis*).

LARVAE. *Head*: Hairs 4-7-C moderately pigmented, long, all at least 5-branched; hair 15-C long, exceeding apex of mental plate. *Thorax*: Roundish in outline, integument densely spiculate, spicules hairlike, simple or branched. *Abdomen*: Integument strongly uniformly spiculate. Hair 8-VII slightly cephalodorsad of 9-VII. *Siphon*: Integument imbricate or spiculate; acus distinct, separate. *Anal Segment*: Hair 3-X single; ventral brush with 6 pairs of hairs.

DISCUSSION. The *Quadrivittatus* Group of 4 species is distinguished by unique features both in the adults (absence of midfemoral and hindfemoral light spots) and in the larvae (ventral brush with 6 pairs of hairs). Since both these characters are primitive ones in the subgenus, this group probably represents the most ancient lineage in the section.

The group is known only in Central America from southern Mexico to central Panama, usually at elevations above 4,000 feet, and is sympatric with the *Allotecnion* Group (fig.5). *A. quadrivittatus* is the only widespread species, occupying the entire known range of the group; *lorraineae* is restricted to the Sierra Madre del Sur and Sierra Madre de Chiapas in Mexico, where it is sympatric with *quadrivittatus*; *spinus* and *brevis* are sympatric with *quadrivittatus* in the southern part of the range, *spinus* in the mountains of Costa Rica and western Panama, and *brevis* apparently only in western Panama.

17. *Aedes* (Howardina) *quadrivittatus* (Coquillett)

Figs.5,8,36,37

1902. *Culex quadrivittatus* Coquillett, 1902:292. TYPE: Holotype ♀, Chacula (Huehuetenango), Guatemala, elev. 6600 ft, 13 June 1902, Gustav Eisen [USNM, 6560].

Aedes (Howardina) *quadrivittatus* of Bonne and Bonne-Wepster (1925:369); Carpenter, Galindo and Trapido (1952:163); Horsfall (1955:471); Trapido, Galindo and Carpenter (1955:530,537,

538); Vargas (1956:22); Trapido and Galindo (1957:122,125,130); Galindo (1964:34,56); Belkin, Schick and Heinemann (1965:28); Forattini (1965:401-403); Diaz Najera (1966b:63).
Aedes quadrivittatus of Dyar and Knab (1907:11); Theobald (1910:486); Picado (1913:353); Howard, Dyar and Knab (1917:852-853); Dyar (1918:73); Kumm, Komp and Ruiz (1940:400, 417); Arnett (1949:238); Galindo, Carpenter and Trapido (1955:163); Stone and Knight (1956:224); Blanton and Peyton (1958:31).
Aedes (Howardina) quadrivittatus in part of Dyar (1928:229-230); Edwards (1932:155); Lane (1939:100; 1953:40); Stone, Knight and Starcke (1959:174).
Culex quadrivittatus of Blanchard (1905:628); Theobald (1905:29; 1910:395).

FEMALE. Wing: 3.33 mm. Proboscis: 2.16 mm. Forefemur: 1.8 mm. Abdomen: about 3.06 mm. *Head*: Light decumbent scales golden on median stripe and short orbital line; sides and venter creamy. Erect scales on occiput dull golden. Palpus about 0.2 of proboscis, with a few white scales apically and mesally on segment 4. Basal flagellar segment with dark scales. *Thorax* (fig.8): Mesonotal light scales golden; outer dorsocentral line complete, only slightly expanded at fossa, merging with lateral marginal line at level of humeral bristles; lateral marginal line long, extending from humeral bristles to wingbase. Median scutellar lobe with broad dark scales laterally and narrow median golden scales from base to apex; lateral lobe with a few linear golden scales. Paratergite with pale golden linear scales. *Apn* with narrow anterior and broader posterior pale golden scales; *ppn* with only an upper patch of pale golden linear scales; *psp* patch pale golden, linear; *ssp* patch with creamy broad scales; other pleural patches white, scales broad with distribution as in the group. *Legs*: Forefemur and midfemur predominantly dark anteriorly except for a few basal creamy scales, proximal half of posterior surfaces creamy and distal dark; hindfemur creamy up to 0.67 on both sides, rest dark. Foretarsus with a few basal white scales on segments 1,2; midtarsus with short, often incomplete basal white rings on 1,2; hindtarsus with moderate white rings on 1-3; rest of tarsi dark. *Haltere*: Stem pale, knob with dark scales basally; fringe whitish. *Abdomen*: Sternites with broad, V-shaped basal creamy patch and rest dark; with a few apical creamy scales on II-V.

MALE. Wing: 3.42 mm. Proboscis: 2.43 mm. Forefemur: 1.98 mm. Essentially similar to female in color. Submedian dark area of head narrower than in female. Median scutellar lobe with larger number of golden scales.

MALE GENITALIA (fig.36). As figured; diagnostic characters as in the key. Ninth tergite lobe prominent, with about 3-5 strong bristles. Sidepiece length 3.0 of median width. Apical seta of claspette on a short basal tubercle, broader than long. Clasper about 0.6 of sidepiece, with 1,2 subapical hairs; spiniform short, about 0.25 of clasper. Aedeagus shorter than proctiger; dorsal sclerotization more or less deeply emarginate, producing distinct lateral apical lobes.

PUPA (fig.36). Abdomen: 3.56 mm. Trumpet: 0.51 mm; index about 5.3-5.5. Paddle: 0.81 mm. Readily separated from *brevis* by the elongate paddle with produced apex; from *spinosus* by hair 9-VIII usually at least 8-branched. Chaetotaxy as figured, hairs moderately to darkly pigmented. *Cephalothorax*: Mesonotum between trumpets moderately pigmented, lateral areas deeper; metanotum strongly pigmented; trumpet strongly contrasting. Hair 1(1, 1-3), 2(1, 1-2), 3(1), 4(2, 2-3), 5(2), 6(1), 7(2), 8(2, 1-3), 9(1), 10(6, 2-7), 11(1, 1-2), 12(1, 1-3). *Abdomen*: Tergite I strongly pigmented except for usual membranous areas; segments II-IV strongly pigmented and imbricate, rest progressively lighter caudad. Segment I: hair 1(8-13 primary branches, each with several secondary branches), 2(1, 1-6), 3(1), 4(2, 2-3), 5(2, 1-3), 6(1, 1-2), 7(1, 1-2), 9(1). Segment II: hair 0(1), 1(5, 2-10), 2(1, 1-3), 3(1), 4(3, 2-5), 5(1, 1-2), 6(1), 7(1, 1-2), 9(1). Segment III: hair 0(1), 1(1, 1-3), 2(1, 1-2), 3(1),

4(1, 1-2), 5(1, 1-2), 6(1), 7(2, 1-3), 8(2, 1-3), 9(1), 10(1), 11(1), 14(1). Segment IV: hair 0(1), 1(1, 1-2), 2(1, 1-2), 3(2), 4(1, 1-2), 5(2), 6(1), 7(1, 1-3), 8(2, 1-3), 9(1), 10(1), 11(1), 14(1). Segment V: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1, 1-2), 5(2, 1-2), 6(1), 7(2, 2-4), 8(2, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1, 1-2), 6(1, 1-3), 7(1, 1-2), 8(2, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1, 1-2), 4(1), 5(1), 6(1, 1-2), 7(1), 8(1, 1-2), 9(4, 3-6), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(9, 7-11), 14(1, 1-2). *Paddle*: Moderately to deeply pigmented, midrib darker; apex distinctly produced; external margin serrate; hair 1 slender. Male genital lobe extending to 0.4 of paddle, female genital lobe to 0.31.

LARVA (fig.37). Head: 0.86 mm. Siphon: 0.97 mm. Anal Saddle: 0.27 mm. Readily separated from *spinosus* and *brevis* by the siphon without distinct spicules and hair 12-C double; from *lorraineae* by hair 5-C usually 5-branched. Chaetotaxy as figured, hairs moderately to darkly pigmented. *Head*: Width subequal to length; pigmentation moderate except around mouthparts where it is deeper. Mental plate with a strong median tooth and 11 distinct teeth (11-12) on each side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(8, 8-11), 5(6, 5-7), 6(7, 5-10), 7(9, 8-15), 8(1), 9(5, 4-6), 10(2), 11(12, 10-17), 12(2, 2-4), 13(1), 14(12, 11-17), 15(3, 2-3). *Antenna*: Length about 0.45 of head; pigmentation moderate. All hairs single except 1-A which is branched (3, 2-3), and at 0.5 from base. *Thorax*: Integument with simple or branched hairlike spicules. Stellate hairs with many barbed branches; long hairs barbed and with attenuate apices. Prothorax: hair 0(19, 13-26), 1(5, 5-8), 2(1), 3(9, 8-11), 4(3, 3-4), 5(2, 1-3), 6(1), 7(2), 8(16, 16-20), 9(9, 7-10), 10(1), 11(2, 1-3), 12(1), 13(24, 20-27), 14(38, 38-48). Mesothorax: hair 1(11, 10-16), 2(1), 3(1), 4(1), 5(1), 6(6, 5-6), 7(1), 8(8, 6-9), 9(9, 7-10), 10(1), 11(1), 12(1), 13(6, 3-8), 14(8, 7-12). Metathorax: hair 1(14, 11-18), 2(1), 3(4, 3-7), 4(15, 12-20), 5(15, 13-20), 6(1), 7(8, 7-10), 8(7, 4-8), 9(5, 5-7), 10(1), 11(1), 12(1), 13(17, 16-23). *Abdomen*: Integument and stellate hairs as on thorax. Segment I: hair 1(21, 16-25), 2(21, 19-28), 3(1), 4(1), 5(14, 14-19), 6(3, 3-4), 7(1), 9(4, 3-6), 10(1), 11(18, 16-24), 13(10, 8-17). Segment II: hair 0(1), 1(18, 17-22), 2(22, 17-28), 3(1), 4(1), 5(18, 16-21), 6(3, 3-5), 7(8, 7-9), 8(1), 9(6, 5-8), 10(1), 11(1), 12(1), 13(14, 12-19). Segment III: hair 0(1), 1(21, 18-25), 2(18, 16-26), 3(1), 4(1), 5(21, 16-26), 6(1), 7(10, 8-11), 8(1), 9(12, 7-15), 10(1), 11(1), 12(1), 13(20, 17-21), 14(1). Segment IV: hair 0(1), 1(20, 18-27), 2(17, 16-27), 3(1), 4(1), 5(21, 15-24), 6(1), 7(8, 8-10), 8(1), 9(16, 10-16), 10(1), 11(1), 12(1), 13(20, 15-21), 14(1). Segment V: hair 0(1), 1(21, 19-27), 2(16, 16-22), 3(1), 4(1), 5(20, 14-20), 6(1), 7(9, 8-12), 8(1), 9(16, 11-19), 10(1), 11(1), 12(1), 13(18, 14-20), 14(1). Segment VI: hair 0(1), 1(17, 17-23), 2(18, 14-21), 3(1), 4(1), 5(17, 15-19), 6(1), 7(9, 8-13), 8(1), 9(15, 10-16), 10(1), 11(1), 12(1), 13(15, 11-15), 14(1). Segment VII: hair 0(1), 1(18, 16-21), 2(16, 14-19), 3(1), 4(1), 5(16, 9-19), 6(6, 4-7), 7(2, 2-3), 8(2, 1-3), 9(9, 8-14), 10(1), 11(1), 12(1), 13(4, 3-5), 14(1). *Segment VIII*: Comb scales 16(14-20), deeply pigmented, elongate; lateral fringes not extending to apex. Hair 0(1), 1(11, 9-14), 2(1), 3(8, 6-10), 4(1), 5(5, 5-6), 14(1). *Siphon*: Index about 4.0-4.2; integument imbricate, moderately to deeply pigmented, with darker basal ring. Pecten with 17(13-18) teeth extending to 0.4 and terminating before hair 1-S; individual tooth long, pointed, with basal denticles. Hair 1(3, 3-4), 2(1), 3-5 not visible, 6(1), 7(1), 8(2, 1-2), 9(1). *Anal Segment*: Saddle deeply pigmented and imbricate; caudal margin with spines of varying length, long ones predominating. Gills long, subequal, as long as ventral brush. Hair 1(2), 2(5, 4-5), 3(1), 4a(4, 3-4), 4b(3, 2-3), 4c(3, 2-4), 4d(3, 2-4), 4e(3, 3-4), 4f(3, 2-4).

SYSTEMATICS. *A. quadrivittatus* is the only species occupying the entire range

of the *Quadrivittatus* Group from the southern end of the Sierra Madre Oriental in Mexico to central Panama. I have seen no specimen of *quadrivittatus* from eastern Panama and all material from South America, formerly reported as this species, actually belongs to new species in the Eleanorae Group. *A. quadrivittatus* is readily differentiated in all stages from the 3 other members of the group which have restricted distributions, all peripherally sympatric with *quadrivittatus*. Its closest relative is undoubtedly *lorraineae* (see). Very little variation is apparent throughout the wide known distribution of *quadrivittatus* except at the northern end in Mexico where the light thoracic scaling of the adults tends to be more yellowish or creamy. No significant population differentiation in the immature stages has been detected in the relatively large sample examined.

BIONOMICS. *A. quadrivittatus* apparently breeds only in epiphytic bromeliads, primarily in cloud forest areas at elevations above 4,000 feet. Females are readily attracted to human bait and display a distinct preference for feeding in the forest canopy (Carpenter, Galindo and Trapido 1952:163). Recently an unidentified arbovirus has been isolated from *quadrivittatus* in Panama (Galindo 1964:34).

DISTRIBUTION (fig.5). Cordilleras of Middle America in Mexico (southern part of Sierra Madre Oriental and eastern end of Sierra Madre del Sur), Guatemala, Honduras, El Salvador, probably Nicaragua, Costa Rica and Panama (western part) at elevations varying from about 4000 ft to 8400 ft. Material examined: 321 specimens; 15 ♂, 42 ♀, 43 pupae, 221 larvae; 31 individual rearings (6 pupal, 13 larval, 12 incomplete).

COSTA RICA. *Alajuela*: Poasito, 14 Nov 1962, C.L. Hogue and W.A. Powder (CR 23), 1 lp♀ (23-105), 1 L [UCLA]. Volcan Poas, 1 p♀ (156), 1 ♀ [USNM]; Summit, 9 July 1963, C.L. Hogue, 1 L (CR 145) [UCLA]. *Cartago*: Elev. 1500 m, C. Picado, 2 ♀ [USNM]. Cervantes, 9 Nov 1962, J.N. Belkin, C.L. Hogue and W.A. Powder, 3 L (CR 13) [UCLA]. Cipreses, 4 ♂, 2 ♀, 9 L, 31 [USNM]. La Sierra, elev. 6300-8400 ft, 24 Nov 1962, C.L. Hogue and W.A. Powder, 1 IP (49-107), 1 ♂, 7 L (CR 49), 1 lp♂ (51-105), 1 lp♀ (51-103), 2 IP (51-107,110), 2 ♂, 6 P, 1 p, 25 L (CR 51), 1 lp♂ (52-105), 2 IP (52-106,108), 12 L (CR 52), 3 lp♂ (53-101-103), 1 P, 2 L (CR 53), 1 lp♂ (54-103), 1 lp♀ (54-106), 5 IP (54-101,102,104,105,107), 3 P, 1 p, 117 L (CR 54) [UCLA].

EL SALVADOR. Los Esesmiles, H.W. Kumm, 2 L [USNM].

GUATEMALA. *Chimaltenango*: San Andres Semetabaj, 17 July 1965, Cowsill (GUA 50), 1 lp♀ (50-10) [UCLA]. Solola, 30 June 1964, J.N. Belkin and J.E. Zavortink (GUA 15), 2 lp♂ (15-10, 12), 1 lp♀ (15-11), 2 IP (15-13,14), 3 L [UCLA]. *Huehuetenango*: Chacula, elev. 6600 ft, 13 June 1902, G. Eisen, type series, 6 ♀ [USNM]. *Locality not specified*: Sept 1902, G. Eisen, 1 ♀; 1 ♂, 3 ♀ [USNM].

HONDURAS. Tegucigalpa, 17 July 1945, 1 lp [USNM].

MEXICO, *Chiapas*: Paval, 28 A (Diaz Najera 1966b:61). Teopisca, 19 Aug 1964, E. Fisher and D. Verity, 10 L (MEX 132) [UCLA]. Triunfo, 125 A (Diaz Najera 1966b:61). *Morelos*: (Vargas 1956:22). *Oaxaca*: Ixtlan de Juarez, Vivero Rancho Teja, elev. 7200 ft, 12 Aug 1966, D.A. Schroeder (MEX 430), 1 p♂ (430-105), 4 p♀ (430-101-104), 12 ♀ (MEX 433) [UCLA]. *Tamaulipas*: Rancho del Cielo, 4 Apr 1963, Trevino, 2 ♀ [USNM]. *Veracruz*: Banderilla, Feb 1945, G. Lissmann, 2 ♂ [UCLA].

PANAMA. *Bocas del Toro*: near Almirante, 1952-53, 2297 ♀ (Trapido and Galindo 1957:122, 125). La Zorra, elev. 4400 ft, 5 Apr 1963, A. Quinonez, 2 ♀ (PA 174), 1 ♀ (PA 175) [UCLA]. *Panama*: Cerro Campana, 28 Aug 1963, A. Quinonez, 1 ♀ (PA 537) [UCLA].

18. *Aedes* (Howardina) *lorraineae* Berlin, n.sp.

Figs.5,8,38

TYPES: Holotype ♀ (MEX 433), Vivero Rancho Teja, Ixtlan de Juarez, Oaxaca, Mexico, 7200 ft, biting collection, 12 Aug 1966, D.A. Schroeder [USNM]. Paratypes: 7 ♀ (MEX 433), same data as holotype [USNM, BM, UCLA]. This species is dedicated to the memory of Mrs. Lorraine Belkin.

FEMALE. Wing: 3.85 mm. Proboscis: 2.62 mm. Forefemur: 2.19 mm. Abdomen: about 3.15 mm. Generally similar to *quadrivittatus* and other members of the group, differing primarily in the following. *Head*: Light decumbent scales on median stripe and short orbital line creamy. Erect scales creamy. Palpus about 0.2 of proboscis, with a few white scales on mesal surface of segment 4. Basal flagellar segment with a few white scales on dorsomesal surface. *Thorax* (fig.8): Mesonotal light lines creamy to pale golden; outer dorsocentral line complete, broadly joined anteriorly in fossa to entire lateral prescutal area and reaching to scutellum; lateral marginal line shorter, extending from scutal angle to wingbase. Narrow light scales on median scutellar lobe creamy; lateral lobes with a few narrow creamy scales. Paratergite and *psp* with moderately broad, white scales; *apn* patch creamy; upper *ppn* with predominantly broad creamy scales; lower *ppn* white, adjoining *ssp* patch; other pleural patches white, distributed as in the group. *Legs*: Forefemur and midfemur predominantly dark anteriorly except for scattered creamy scales up to proximal 0.5, proximal 0.5 of posterior surfaces creamy, extending distally as narrow line, rest dark; hindfemur creamy proximally to 0.6 on both sides and rest dark. Foretarsus with basal white scales on segment 1; midtarsus with short incomplete white rings on 1,2; hindtarsus with moderately broad white rings on 1-3. *Haltere*: Stem pale, knob predominantly white, with a few basal dark scales. *Abdomen*: Sternites with broad V-shaped basal white patches; apical white scales numerous on II-IV, few on V and absent on distal segments.

MALE unknown and PUPA imperfectly known.

LARVA (fig.38). Head: 0.81 mm. Siphon: 0.87 mm. Anal Saddle: 0.27 mm. Diagnostic characters as in the key. Readily separated from *quadrivittatus* by hair 5-C usually only 3,4-branched; from *brevis* and *spinosus* by the absence of spicules on siphon. *Head*: Mental plate with a strong median tooth and 11 distinct teeth (10-12) on each side, often a small detached tooth at base. Hair 0(1), 1(1), 3(1), 4(7, 5-11), 5(3, 3-4), 6(5, 5-6), 7(6, 6-9), 8(1), 9(2, 1-3), 10(2), 11(11, 9-17), 12(2, 1-2), 13(1), 14(8, 6-13), 15(2, 2-3). *Antenna*: Length about 0.33 of head; uniformly moderately pigmented, with a few scattered spicules; hairs simple except 1(2, 2-3). *Thorax*: Integument predominantly with simple hairlike spicules. Stellate hairs with many unequal barbed branches; long hairs barbed and with attenuate apices. Prothorax: hair 0(16, 13-17), 1(6, 4-6), 2(1), 3(8, 6-10), 4(4, 2-4), 5(2), 6(1), 7(2), 8(16, 14-19), 9(8, 7-9), 10(1), 11(2, 1-2), 12(1), 13(22, 19-27), 14(40, 38-56). Mesothorax: hair 1(11, 10-18), 2(1), 3(1), 4(1), 5(1), 6(6, 4-6), 7(1), 8(7, 6-8), 9(6, 6-9), 10(1), 11(1, 1-2), 12(1), 13(6, 5-9), 14(7, 6-9). Metathorax: hair 1(13, 10-18), 2(1), 3(4, 4-6), 4(10, 10-17), 5(13, 8-16), 6(1), 7(7, 4-8), 8(6, 6-9), 9(5, 4-7), 10(1), 11(1, 1-2), 12(1), 13(20, 14-22). *Abdomen*: Long and stellate hairs as in thorax. Segment I: hair 1(18, 15-21), 2(16, 14-22), 3(1), 4(1), 5(12, 10-16), 6(3, 2-3), 7(1), 9(5, 4-7), 10(1), 11(17, 14-21), 13(15, 9-21). Segment II: hair 0(1), 1(17, 13-20), 2(20, 12-23), 3(1), 4(1, 1-2), 5(16, 13-19), 6(3), 7(8, 5-10), 8(1), 9(6, 6-9), 10(1), 11(1), 12(1), 13(14, 11-17). Segment III: hair 0(1), 1(20, 15-22), 2(16, 14-21), 3(1), 4(1), 5(16, 13-20), 6(1, 1-2), 7(10, 8-11), 8(1), 9(10, 8-16), 10(1), 11(1), 12(1), 13(16, 16-19), 14(1). Segment IV: hair 0(1), 1(20, 15-23), 2(19, 15-19), 3(1), 4(1), 5(16, 14-22), 6(1, 1-2), 7(10, 7-12), 8(1), 9(12, 10-18), 10(1), 11(1), 12(1), 13(17, 13-21), 14(1). Segment V: hair 0(1), 1(19, 14-21), 2(18, 12-18), 3(1), 4(1), 5(16, 11-17), 6(1, 1-2), 7(11, 8-11), 8(1), 9(12, 10-17), 10(1), 11(1), 12(1), 13(15, 12-19), 14(1). Segment VI: hair

0(1), 1(18, 12-23), 2(17, 12-18), 3(1), 4(1), 5(16, 12-17), 6(1, 1-2), 7(10, 8-12), 8(1), 9(13, 8-18), 10(1), 11(1), 12(1), 13(12, 10-19), 14(1). Segment VII: hair 0(1), 1(18, 13-23), 2(17, 10-18), 3(1), 4(1), 5(16, 13-20), 6(4, 3-5), 7(2, 2-3), 8(2, 2-4), 9(8, 6-11), 10(1), 11(1), 12(1), 13(4, 3-4), 14(1). *Segment VIII*: Comb scales usually 16(14-20), moderately pigmented, their lateral fringes not extending to apex. Hair 0(1), 1(8, 7-16), 2(1), 3(8, 7-9), 4(1), 5(6, 5-8), 14(1, 1-2). *Siphon*: Index 3.3-3.6; integument imbricate, moderately pigmented, with darker basal ring. Pecten teeth usually 16(13-18), extending to 0.4. Hair 1(4, 3-5), 2(1), 3-5 not visible, 6(1), 7(1), 8(2, 1-2), 9(1). *Anal Segment*: Saddle moderately pigmented. Gills subequal, narrow, as long as ventral brush. Hair 1(2, 2-3), 2(5, 4-6), 3(1), 4a(3, 3-4), 4b(3, 2-3), 4c(3, 2-3), 4d(3, 2-3), 4e(3, 2-3), 4f(3, 2-3).

SYSTEMATICS. *A. lorraineae* is undoubtedly closely related to *quadrivittatus*. It is differentiated in the female most conspicuously by the white scales on the first flagellar segment and generally whiter scales on the mesonotum and pleura. The association of the immature stages with the females is presumptive only since all the rearings are incomplete. The larva described here, although very similar to *quadrivittatus*, is distinct from those of Mexican and other populations of the latter in the smaller number of branches in head hair 5. The pupal stage is also in general similar to *quadrivittatus* but cannot be described at this time since only a few imperfect whole pupae from incomplete rearings are available. *A. lorraineae* is known at present only from the Sierra Madre del Sur and the Sierra Madre de Chiapas in Mexico at elevations above 7,000 feet. In the eastern part of this range, in the states of Oaxaca and Chiapas, *lorraineae* is sympatric with *quadrivittatus*. In one biting-landing collection (MEX 433) in Oaxaca where the 2 species were taken in approximately equal numbers there is no indication of intergradation between *lorraineae* and *quadrivittatus*. This supports my interpretation that *lorraineae* is a distinct species and not a geographical isolate of *quadrivittatus*.

BIONOMICS. Immature stages of *lorraineae* have been collected in epiphytic bromeliads only. Females of this species are apparently readily attracted to humans.

DISTRIBUTION (fig.5). Sierra Madre del Sur and Sierra Madre de Chiapas in Mexico at elevations above 7000 ft. Material examined: 75 specimens; 11 ♀, 5 pupae, 59 larvae; 5 incomplete individual rearings.

MEXICO. *Chiapas*: 27 Mar 1961, R.B. Eads, 1 L [USNM]. *Guerrero*: Omilteme, 8 Sept 1965, D.A. Schroeder, 3 ♀ (MEX 361A), 3 IP (362-21-23), 24 L (MEX 362) [UCLA]. *Oaxaca*: Ixtlan de Juarez, El Punto, elev. 7700 ft, 13 Aug 1966, D.A. Schroeder, 4 L (MEX 434); Vivero Rancho Teja, elev. 7200 ft, 12 Aug 1966, D.A. Schroeder, 2 IP (428-10,11), 9 L (MEX 428), 4 L (MEX 429), 9 L (MEX 430), 3 L (MEX 431), 8 ♀ (MEX 433, type series) [USNM, BM, UCLA].

19. *Aedes* (Howardina) *brevis* Berlin, n.sp.

Figs.5,9,39,40

TYPES: Holotype ♂ (PA 171-104) with associated pupal skin and genitalia slide, La Zorra, Chiriquisito, Chiriqui Grande, Bocas del Toro, Panama, 4400 ft, 5 Apr 1963, A. Quinonez [USNM]. Allotype ♀ (PA 171-102) with associated pupal skin, same data as holotype [USNM]. Paratypes: 1 ♀ (171-105), 2 IP (171-101,103), 2 P, 18 L, same data as holotype [UCLA].

FEMALE. Wing: 3.78 mm. Proboscis: 2.7 mm. Forefemur: 2.34 mm. Abdomen: about 3.1 mm. Generally similar to *quadrivittatus* and other members of the group; differing primarily in the following. *Head*: Palpus about 0.15 of proboscis; with dis-

tinct apical white scales on segment 4. *Thorax* (fig.9): Outer dorsocentral line incomplete, arising at anterior 0.33 and reaching to scutellum; lateral marginal line long, extending from anterior promontory to wingbase, slightly curved inwards at lateral prescutal area. Lateral scutellar lobes with a few narrow dark scales. Paratergite and *psp* with narrow creamy scales; other pleural scale patches as in *quadrivittatus*, all dull white. *Legs*: Forefemur dark anteriorly except for a few basal dingy scales, proximal 0.5 of posterior surface dingy white, extending distally as narrow line bordered by dark scales; midfemur dark anteriorly, proximal 0.6 of posterior surface dingy white, distal dark; hindfemur dingy white proximally to 0.67 on both sides, rest dark. Foretarsus with basal white scales on segments 1,2; midtarsus with short incomplete white rings on 1,2; hindtarsus with broader white rings on 1-3, last covering about 0.65 of segment. *Haltere*: Stem pale; knob predominantly white, with a few dorsal dark scales. *Abdomen*: Sternites with broad V-shaped basal creamy patches; apical light scales apparent on II,III.

MALE. Wing: 3.33 mm. Proboscis: 2.89 mm. Forefemur: 2.28 mm. Essentially similar to the female in color.

MALE GENITALIA (fig.39). As figured; diagnostic characters as in the key. Ninth tergite lobe indistinct, with 8-10 moderate bristles. Sidepiece length about 3.0 of median width. Clasper about 0.5 of sidepiece, with 1,2 subapical hairs; spiniform short, length about 0.25 of clasper. Apex of aedeagus with slender horns bent dorsad.

PUPA (fig.39). Abdomen: 3.78 mm. Trumpet: 0.54 mm; index about 6.0. Paddle: 0.7 mm. Readily separated from other species of group by the deeply emarginate paddle. Chaetotaxy as given below, hairs moderately to darkly pigmented. *Cephalothorax*: Mesonotum lightly pigmented between trumpets, lateral areas darker; metanotum moderately pigmented. Hair 1(1, 1-2), 2(1), 3(1), 4(2), 5(2), 6(1), 7(2, 1-2), 8(2, 2-3), 9(1), 10(12, 12-14), 11(1), 12(1, 1-3). *Abdomen*: Tergite I uniformly moderately pigmented except for usual membranous areas; other segments moderate, pigmentation progressively lighter caudad. Segment I: hair 1(10-20 primary branches, each with secondary branches), 2(2, 1-4), 3(1), 4(3, 2-4), 5(3, 2-5), 6(1), 7(1, 1-2), 9(1); in some hair 10(1) present. Segment II: hair 0(1), 1(16, 12-20), 2(1, 1-2), 3(1), 4(3, 1-3), 5(2, 1-3), 6(1), 7(1), 9(1), 11(1). Segment III: hair 0(1), 1(2, 2-3), 2(1), 3(1), 4(1, 1-2), 5(1, 1-5), 6(1), 7(1, 1-2), 8(1), 9(1), 10(1), 11(1), 14(1). Segment IV: hair 0(1), 1(2), 2(1), 3(2, 1-2), 4(1), 5(2), 6(1), 7(1), 8(1), 9(1), 10(1), 11(1), 14(1). Segment V: hair 0(1), 1(2, 1-2), 2(1), 3(1), 4(1), 5(2), 6(1), 7(2, 1-3), 8(1), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1), 5(1), 6(1), 7(2, 1-6), 8(1), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1), 5(1), 6(2, 1-3), 7(1), 8(1, 1-2), 9(7, 5-8), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(11, 11-14), 14(1). *Paddle*: Uniformly lightly pigmented, midrib slightly darker; deeply emarginate; external margin serrate; hair 1-P single. Male genital lobe extending to about 0.5 of saddle, female genital lobe to 0.35.

LARVA (fig.40). Head: 0.96 mm. Siphon: 0.6 mm. Anal Saddle: 0.3 mm. Readily separated from other members of the group by hair 5-C usually with 18 branches (11-22) and short siphon with an index of about 2.0. *Head*: Mental plate with a strong median tooth and 10 distinct teeth (9-10) on each side, often a small detached tooth at base. Hair 0(1), 1(1), 3(1), 4(16, 13-20), 5(18, 11-22), 6(12, 9-19), 7(15, 11-21), 8(4, 1-7), 9(9, 6-18), 10(6, 3-8), 11(24, 18-25), 12(8, 5-12), 13(1), 14(19, 15-22), 15(2, 2-4). *Antenna*: Length about 0.35 of head; shaft uniformly moderately pigmented, with a few scattered spicules; hairs simple except 1(2, 2-3). *Thorax*: Integument with simple and branched, hairlike spicules. Stellate hairs with many unequal barbed branches; long hairs barbed and with attenuate apices. Prothorax: hair

0(24, 19-24), 1(12, 10-14), 2(1, 1-2), 3(14, 13-23), 4(4, 3-6), 5(2, 2-3), 6(1), 7(3, 2-3), 8(21, 16-26), 9(7, 6-12), 10(1), 11(2, 1-2), 12(1), 13(30, 24-31), 14(38, 34-43). Mesothorax: hair 1(21, 15-33), 2(1), 3(1), 4(1), 5(1, 1-2), 6(6, 6-9), 7(1), 8(7, 5-7), 9(9, 7-10), 10(1), 11(1, 1-2), 12(1), 13(16, 9-16), 14(16, 15-21). Metathorax: hair 1(28, 22-30), 2(1), 3(16, 12-19), 4(5, 4-5), 5(12, 11-15), 6(1), 7(6, 4-9), 8(14, 10-18), 9(5, 5-8), 10(1), 11(1), 12(1), 13(19, 19-35). *Abdomen*: Stellate hairs as in thorax. Segment I: hair 1(29, 29-32), 2(22, 18-31), 3(1), 4(1, 1-3), 5(18, 14-23), 6(3, 1-4), 7(1), 9(7, 5-8), 10(1), 11(22, 17-22), 13(26, 23-27). Segment II: hair 0(1), 1(26, 24-40), 2(22, 15-26), 3(1), 4(1), 5(18, 16-23), 6(3, 3-4), 7(13, 5-14), 8(1), 9(13, 9-15), 10(1), 11(1), 12(1), 13(25, 21-26). Segment III: hair 0(1), 1(26, 24-35), 2(18, 15-22), 3(1), 4(1), 5(18, 17-22), 6(3, 2-3), 7(14, 11-15), 8(1), 9(16, 12-16), 10(1), 11(1), 12(1), 13(21, 19-25), 14(1). Segment IV: hair 0(1), 1(26, 24-29), 2(16, 16-20), 3(1), 4(1), 5(19, 15-21), 6(2), 7(11, 11-18), 8(1), 9(15, 15-18), 10(1), 11(1), 12(1), 13(21, 20-34), 14(1). Segment V: hair 0(1), 1(25, 24-37), 2(18, 15-20), 3(1), 4(1), 5(18, 16-21), 6(2, 2-3), 7(12, 9-18), 8(1), 9(16, 14-24), 10(1), 11(1), 12(1), 13(19, 18-34), 14(1). Segment VI: hair 0(1), 1(27, 24-38), 2(18, 15-19), 3(1), 4(1), 5(16, 14-20), 6(2), 7(12, 11-14), 8(1), 9(16, 14-20), 10(1), 11(1), 12(1), 13(20, 17-22), 14(1). Segment VII: hair 0(1), 1(25, 23-30), 2(17, 14-22), 3(1), 4(1), 5(16, 14-18), 6(7, 5-7), 7(2, 1-2), 8(3, 2-4), 9(19, 14-20), 10(1), 11(1), 12(1), 13(19, 17-23), 14(1, 1-2). *Segment VIII*: Comb scales usually 16(14-17), moderately pigmented, their lateral fringes not extending to apex. Hair 0(1), 1(18, 15-21), 2(1), 3(7, 6-9), 4(1), 5(16, 15-20), 14(1). *Siphon*: Index about 2.0; integument moderately pigmented, with darker basal ring and with rows of small hairlike spicules. Pecten teeth usually 9(7-16), extending to 0.3. Hair 1(5, 4-6), 2(1), 3-5 not visible, 6(1), 7(1), 8(1, 1-2), 9(1). *Anal Segment*: Saddle moderately pigmented, with a darker basal ring and with small spicules; caudal margin with spines of varying length. Gills about 2.0 of saddle length, narrow and subequal. Hair 1(2, 2-3), 2(6, 4-6), 3(1), 4a(4, 3-5), 4b(3, 2-3), 4c(3, 3-4), 4d(4), 4e(4, 3-5), 4f(4, 3-5).

SYSTEMATICS. The adults of *brevis* cannot be differentiated from the apparently closely related *spinosus* but the immature stages of the 2 species are strikingly differentiated as indicated in the diagnosis and in the keys. The association of all the stages is undoubtedly correct although no complete larval rearings were made. At present, *brevis* is known only from northern Panama where it has been found in the same locality as *quadrivittatus* and *spinosus* but not in the same collections.

BIONOMICS. Immature stages of *brevis* have been collected in epiphytic bromeliads at elevations above 4,000 feet. All 5 known adults were reared but it is possible that the 2 females taken in biting-landing collections in Panama provisionally identified as *spinosus* are actually *brevis*.

DISTRIBUTION (fig.5). Chiriqui mountains of Panama at elevations above 4000 ft. Material examined: 58 specimens; 3 ♂, 2 ♀, 10 pupae, 43 larvae; 8 individual rearings (1 larval, 4 pupal, 3 incomplete).

PANAMA. *Bocas del Toro*: La Zorra, elev. 4400 ft, 5 Apr 1963, A. Quinonez (PA 171, type series), 1 l♂ (171-105), 1 p♂ (171-104), 1 p♀ (171-102), 2 IP (171-101,103), 2 P, 18 L; 6 Apr 1963, A. Quinonez, 18 L (PA 178); 9 Apr 1963, A. Quinonez (PA 183), 1 p♂ (183-101), 1 p♀ (183-103), 1 IP (183-102), 3 L [USNM, UCLA].

20. *Aedes* (Howardina) *spinosus* Berlin, n.sp.

Figs.5,9,41,42

TYPES: Holotype ♀ (CR 13-111) with associated pupal and larval skins, near Cervantes, Cartago, Costa Rica, 9 Nov 1962, J.N. Belkin, C.L. Hogue and W.A. Powder [USNM]. Paratypes: 4 larvae (CR 13), same data as holotype [USNM, UCLA].

FEMALE. Wing: 3.33 mm. Proboscis: 2.32 mm. Forefemur: 1.8 mm. Abdomen: 3.06 mm. Holotype lacking part of hindtarsus, entire left leg and abdomen. Essentially similar to *brevis* in all details, from which it cannot be separated. The only apparent difference is in the pleural scales which are white in *spinosus* and dingy white in *brevis* (fig.9).

MALE. Wing: 3.5 mm. Proboscis: 2.8 mm. Forefemur: 2.15 mm. Essentially similar to female in color.

MALE GENITALIA (fig.41). Diagnostic characters as in the key. Essentially similar to *brevis* in all details.

PUPA (fig.41). Abdomen: 3.25 mm. Trumpet: 0.5 mm; index about 6.0. Paddle: 0.77 mm. Readily separated from *brevis* by the rounded or slightly produced paddle; from *quadrivittatus* by 2-branched hair 9-VII and 5-branched 9-VIII. Hairs moderately to darkly pigmented. *Cephalothorax*: Mesonotum lightly pigmented between trumpets, lateral areas and metanotum slightly darker; trumpets moderately long, strongly contrasting. Hair 10-C with 5 branches; 12-C double. *Abdomen*: Tergite I moderately pigmented except for usual membranous areas; pigmentation of rest of segments moderate, progressively lighter caudad. Hair 1-II 8-branched; hair 5-IV,V long, double, exceeding apex of second tergite following; hair 9-VII distinctly larger than 6-VII, double, long, exceeding apex of tergite; hair 9-VIII long, 5-branched. *Paddle*: Uniformly lightly pigmented, midrib slightly darker; apex rounded or slightly produced; hair 1-P single; external margin serrate. Female genital lobe extending to 0.38 of paddle.

LARVA (fig.42). Head: 0.88 mm. Siphon: 0.88 mm. Anal Saddle: 0.33 mm. Readily separated from *quadrivittatus* and *lorraineae* by the pilose siphon; from *brevis* by the longer siphon and hair 5-C usually 5-branched (4-7). *Head*: Mental plate with a strong median tooth and 11 distinct teeth (11-12) on each side, often a small detached tooth at base. Hair 0(1), 1(1), 3(1), 4(9, 8-11), 5(5, 4-7), 6(8, 6-9), 7(8, 8-11), 8(2, 1-3), 9(7, 5-9), 10(4, 3-5), 11(21, 17-24), 12(8, 4-10), 13(1), 14(16, 15-24), 15(3). *Antenna*: Length about 0.33 of head; shaft moderately pigmented and with a few scattered spicules; hairs simple except 1(2, 2-3) which is at about 0.6 from base. *Thorax*: Integument predominantly with branched, hairlike spicules. Stellate hairs with many unequal barbed branches; long hairs with attenuate apices. Prothorax: hair 0(18, 16-20), 1(5, 5-8), 2(1), 3(11, 10-14), 4(3, 3-5), 5(2), 6(1), 7(2), 8(16, 16-20), 9(6, 4-7), 10(1), 11(2, 2-3), 12(1), 13(31, 20-38), 14(44, 44-60). Mesothorax: hair 1(18, 9-20), 2(1), 3(1), 4(1), 5(1), 6(6, 4-6), 7(1), 8(7, 6-7), 9(7, 4-7), 10(1), 11(2), 12(1), 13(5, 4-7), 14(8, 5-14). Metathorax: hair 1(25, 14-27), 2(1), 3(4, 3-4), 4(18, 14-20), 5(18, 15-20), 6(1), 7(7, 5-8), 8(10, 5-10), 9(5, 4-6), 10(1), 11(1, 1-2), 12(1), 13(20, 18-24). *Abdomen*: Segment I: hair 1(28, 24-33), 2(25, 22-27), 3(1), 4(1), 5(20, 16-23), 6(3), 7(1, 1-2), 9(6, 6-8), 10(1), 11(22, 19-25), 13(24, 20-28). Segment II: hair 0(1), 1(30, 26-34), 2(24, 21-28), 3(1), 4(1), 5(28, 22-31), 6(3), 7(14, 10-14), 8(1), 9(14, 11-16), 10(1), 11(1), 12(1), 13(29, 26-31). Segment III: hair 0(1), 1(30, 22-35), 2(25, 22-29), 3(1), 4(1), 5(28, 22-31), 6(2), 7(16, 10-16), 8(1), 9(20, 11-22), 10(1), 11(1), 12(1), 13(28, 18-32), 14(1). Segment IV: hair 0(1), 1(30, 21-36), 2(27, 20-28), 3(1), 4(1), 5(26, 19-31), 6(2), 7(16, 9-17), 8(1), 9(20, 15-25), 10(1), 11(1), 12(1), 13(27, 20-32), 14(1). Segment V: hair 0(1), 1(34, 23-34), 2(24, 16-28), 3(1), 4(1), 5(26, 20-31), 6(2), 7(16, 9-19), 8(1), 9(21, 16-24),

10(1), 11(1), 12(1), 13(27, 18-28), 14(1). Segment VI: hair 0(1), 1(32, 21-33), 2(23, 17-27), 3(1), 4(1), 5(27, 19-29), 6(2), 7(17, 11-20), 8(1), 9(20, 15-24), 10(1), 11(1), 12(1), 13(20, 16-24), 14(1). Segment VII: hair 0(1), 1(30, 22-34), 2(25, 17-26), 3(1), 4(1), 5(18, 17-24), 6(9, 6-11), 7(2, 2-3), 8(1), 9(22, 10-23), 10(1), 11(1), 12(1), 13(17, 13-20), 14(1). *Segment VIII*: Comb scales usually 16(14-18), moderately pigmented; individual scale long, pointed apically and fringed nearly to tip. Hair 0(1), 1(22, 14-26), 2(1), 3(8, 7-9), 4(1), 5(12, 8-16), 14(1). *Siphon*: Index about 3.2-4.0; moderately pigmented, except for dark basal ring; uniformly covered with rows of small hairlike spicules. Pecten teeth usually 10(10-15), extending to about 0.4 before hair 1-S; individual tooth long, pointed, with basal denticles. Hair 1(5, 4-5), 2(1), 3-5 not visible, 6(1), 7(1), 8(2), 9(1). *Anal Segment*: Saddle moderately pigmented except for darker basal ring; covered with small spicules; caudal margin with serrated spines of varying length. Gills long, subequal, as long as ventral brush. Hair 1(2), 2(6, 6-7), 3(1), 4a(5, 4-5), 4b(3, 3-4), 4c(3, 3-4), 4d(4, 3-4), 4e(3, 3-4), 4f(3, 1-3).

SYSTEMATICS. *A. spinosus* is recognized as a distinct species entirely on the basis of striking and constant features of the immature stages as indicated in the diagnosis. The single individually reared adult (♀) shows no obvious differences from the 5 individually reared specimens of *brevis*. Therefore, the identity of the male and the 5 females listed below is questionable; they could possibly be *brevis*. *A. spinosus* is known at present only from areas of cloud forest above 4,000 feet in Costa Rica and Panama. It is sympatric throughout this range with the dominant *quadrivittatus*. Although the 2 species are reported as being associated in 2 collections of immature stages in Costa Rica (CR 13,54), it is not known if they were actually found together in the same bromeliads. In Panama, *spinosus* has been collected in the same locality as *brevis* but in this instance the immature stages were not associated in a given collection, suggesting an ecological barrier between the 2 species.

BIONOMICS. Immature stages of *spinosus* occur in epiphytic bromeliads. Two females from Panama provisionally identified as *spinosus* were taken in biting-landing collections.

DISTRIBUTION (fig.5). Costa Rica and Panama (Chiriqui mountains) at elevations above 4000 ft. Material examined: 85 specimens; 1 ♂, 6 ♀, 3 pupae, 75 larvae; 2 individual rearings (1 larval, 1 incomplete).

COSTA RICA. *Alajuela*: Volcan Poas, 14 Apr 1938, 2 ♀ [USNM]. *Cartago*: Cervantes, 9 Nov 1962, J.N. Belkin, C.L. Hogue and W.A. Powder (CR 13, type series), 1 ♀ (13-111), 4 L [USNM, UCLA]. Cipreses, 1 ♀ [USNM]. La Sierra, elev. 6300 ft, 24 Nov 1962, C.L. Hogue and W.A. Powder, 55 L (CR 54) [UCLA]. *Locality not specified*: C. Picado, 1 ♂, 2 ♀ [UCLA, USNM].

PANAMA. *Bocas del Toro*: La Sierra, elev. 5400 ft, 8 Apr 1963, A. Quinonez, 5 L (PA 180), 1 ♀ (PA 181) [UCLA]. La Zorra, elev. 4400 ft, 5 Apr 1963, A. Quinonez, 1 L (PA 172); 6 Apr 1963, A. Quinonez, 1 IP (176-103), 1 P, 1 L (PA 176); 7 Apr 1963, A. Quinonez, 5 L (PA 179); 9 Apr 1963, A. Quinonez, 1 ♀ (PA 184) [UCLA].

Sexlineatus Group

FEMALE. *Head*: Median light line on vertex with narrow scales. Proboscis distinctly longer than forefemur. Torus with restricted mesal scale patch. *Thorax*: Mesonotal light lines mostly white, rarely creamy; inner and outer dorsocentral lines complete, subparallel; lateral marginal line continuous; scales on anterior promontory white. Antealar area above paratergite with dark scales. Paratergite with a moderate scale patch extending entire sclerite length. Upper *ppn* entirely covered with scales,

both dark and light scales present; upper *stp* patch quadrate. *Legs*: Distal white spot on anterior surface of midfemur and hindfemur present. Tibiae predominantly dark, with light scales in narrow longitudinal lines. *Wing*: Veins entirely dark scaled. *Abdomen*: Basomedian tergal light markings present on III-VII.

MALE. Palpus with basomedian light scales on segments 4,5.

MALE GENITALIA. Lobe of tergite IX prominent, with 5,6 strong bristles. Sidepieces separated at base by a distance less than width of aedeagus; without any indication of lobes on tergomesal or sternomesal margins. Claspette represented by a conical tubercle. Aedeagus shorter than proctiger; apex smoothly rounded, without any indication of lateral lobes.

PUPA. *Cephalothorax*: Trumpet moderate, index about 5.0, distinctly flared apically; hairs 10,12-C usually with a few branches. *Abdomen*: Hair 5-IV-V moderate, not exceeding the apex of second tergite following; hair 9-VII moderate to strong, distinctly larger than hair 6, exceeding lateral angle of tergite. *Paddle*: Short; apex rounded.

LARVAE. *Head*: Hair 4-C weak, lightly pigmented, at least 4-branched; 5-C single, moderate, strongly pigmented; 6-C heavy, darkly pigmented, triple or double; 7-C moderate, double or triple; 15-C short, barely exceeding base of mental plate. *Thorax*: Roundish in outline; integument strongly spiculate, spicules hairlike, simple. *Abdomen*: Integument densely spiculate. Hair 8-VII slightly cephalodorsad of 9-VII. *Siphon*: Integument imbricate; acus distinct, attached. *Anal Segment*: Hair 3-X double; ventral brush with 5 pairs of hairs.

DISCUSSION. Only 1 species is recognized at this time in the *Sexlineatus* Group although it is evident, as indicated under the species, that there is considerable differentiation in some populations.

The *Sexlineatus* Group shows similarities with the *Whitmorei* Group in adult ornamentation (dark-scaled antealar area) and with the *Allotecnion* Group in the larva (head hair 15-C short). It is the most widespread of all the groups in the section and occurs at lower elevations than any other, particularly in the southern part of its range in Trinidad and in lowland Ecuador where it seems to be the only species of *Howardina* present (fig.4). In the central (Honduras, Panama) and northern (Mexico) portions of its range it occurs at moderate to high elevations and may be sympatric with the *Allotecnion* and *Quadrivittatus* Groups.

21. *Aedes* (*Howardina*) *sexlineatus* (Theobald)

Figs.4,9,43,44

1901. *Stegomyia sexlineata* Theobald, 1901:308. TYPE: Holotype ♀ (102), Agua Santa (St. George), Trinidad, F.W. Urich [BM].

1907. *Stegomyia dominicii* Rangel and Romero-Sierra, 1907:48. TYPE: ♀, Hacienda El Paraiso on Rio Anaucó [Caracas], Venezuela [LU]. **NEW SYNONYMY.**

Aedes (*Howardina*) *sexlineatus* of Dyar (1928:229); Edwards (1932:155); Martini (1935:49); Komp (1936a:57); Lane (1939:101); Martinez and Prosen (1950:38-39); Lane (1953:715-716); Horsfall (1955:471); Martinez and Prosen (1955:23-25); Reyes (1955:74,89); Trapido, Galindo and Carpenter (1955:530,534,537); Vargas (1956:22); Galindo and Trapido (1957:122,124,125,134); Trapido and Galindo (1957:134); Belkin, Schick and Heinemann (1965:69); Forattini (1965:113,232); Cova Garcia, Sutil and Rausseo (1966a:58,287; 1966b:74,141,334-335).

Aedes (*Howardina*) *sexlineata* of Bonne and Bonne-Wepster (1925:367-368).

Aedes sexlineatus of Urich (1913:527,528); Howard, Dyar and Knab (1917:847-849); Dyar (1918:73); Cerqueira (1943b:33); Boshell-Manrique and Osorno-Mesa (1944:173,174,177,178); Del Ponte, Castro and Garcia (1951:240); Aitken (1960:4).

Aedes (Soperia) sexlineata of Anduze (1941:14).

Stegomyia sexlineata of Giles (1902:377); Theobald (1903b:238,239); Blanchard (1905:260).

Gymnometopa sexlineata of Coquillett (1905:183; 1906b:25); Theobald (1907:210; 1910:219); Surcouf and Gonzalez-Rincones (1911:212-213).

Haemagogus sexlineata of Dyar and Knab (1906a:166).

Aedes (Howardina) dominicii of Bonne and Bonne-Wepster (1925:376); Dyar (1928:231); Edwards (1932:155).

Aedes (Soperia) dominicii of Belkin, Schick and Heinemann (1965:74); Cova Garcia, Sutil and Rausseo (1966b:80).

Stegomyia dominicii of Surcouf and Gonzalez-Rincones (1911:131,134-135; 1912:286-287).

FEMALE. Wing: 2.8 mm. Proboscis: 2.2 mm. Forefemur: 1.9 mm. Abdomen: about 2.9 mm. *Head*: Light decumbent scales white. Erect scales whitish on occiput, dark brown on sides and disc. Palpus about 0.2 of proboscis, white scales on mesal surface and apex of segment 4. Torus light brown laterally, darker mesally and with white scales. *Thorax* (fig.9): Mesonotal light lines white to dingy white; inner and outer dorsocentral lines complete from anterior margin to scutellum, scales at level of prescutellar area lighter; lateral marginal line short, narrow from scutal angle to wingbase, scales longer, broader at wingbase. Antealar area above paratergite completely dark scaled. Median scutellar lobe with moderately broad dark scales laterally and with median narrow white scales from base to apex; lateral lobes with narrow dark scales. Paratergite scales broad, white. *Apn* scales white, predominantly broad, a few anterior scales narrower; upper *ppn* with narrow black scales on upper half, light to creamy narrow and broad scales on lower half, extent of black scales varied in different populations; *psp* scales distinct, narrow and creamy in front, broad and white behind; other scale patches pure white, distributed as in group. *Legs*: Forefemur dark anteriorly except for basal creamy scales, dark posteriorly except for a narrow creamy longitudinal line; midfemur mostly dark anteriorly except for basal creamy scales, a narrow mesal white line to middle and a white spot at distal 0.67, proximal 0.6 of posterior surface white, rest dark scaled; hindfemur predominantly dark anteriorly except for broad white line to 0.75 terminating in a white spot, posterior surface white to 0.75, rest dark scaled. Foretibia and midtibia predominantly dark except for anterior, narrow, faint white line; hindtibia dark. Foretarsus with white scales on segments 1,2; midtarsus with short incomplete white rings on 1,2, often a few white scales on 3; hindtarsus with broader white rings on 1-3, occasionally some white scales on segment 4 and sometimes on 5. *Haltere*: Stem pale, knob dark basally, fringe scales white. *Abdomen*: Basomedian tergal scales creamy, silvery on VII. Sternites with broad basal V-shaped pure white patches; apical white scales apparent up to segment V.

MALE. Wing: 2.61 mm. Proboscis: 2.43 mm. Forefemur: 1.8 mm. Essentially similar to female in color.

MALE GENITALIA (fig.43). As figured; diagnostic characters as in the key. Ninth tergite lobe prominent, with 5,6 moderate setae. Sidepiece length about 3.0 of median width. Clasper about 0.5 of sidepiece, spiculate in basal 0.33. Aedeagus short, apex uniformly sclerotized, smoothly rounded, without indication of apical lateral lobes.

PUPA (fig.43). Abdomen: 3.6 mm. Trumpet: 0.43 mm; index about 5.0. Paddle: 0.6 mm. Diagnostic characters as in the key. Chaetotaxy as given below, hairs moder-

ately to darkly pigmented. *Cephalothorax*: Mesonotum moderately pigmented between trumpets, lateral areas and metanotum slightly darker; trumpets contrasting. Hair 1(1), 2(1), 3(1), 4(3, 2-5), 5(2, 2-3), 6(1, 1-2), 7(2, 2-3), 8(2, 1-4), 9(1), 10(4, 1-7), 11(1, 1-2), 12(3, 1-4). *Abdomen*: Tergite I uniformly strongly pigmented except for usual light membranous area; segments II-VIII with imbricate integument, strongly pigmented, progressively lighter caudad. Segment I: hair 1(6-13 primary branches, each with many secondary ones), 2(1, 1-2), 3(1, 1-2), 4(2, 2-4), 5(3, 1-6), 6(1, 1-2), 7(1, 1-4), 9(1, 1-3), 10(1-2; present in some), 11(1-4, present in some). Segment II: hair 0(1), 1(2, 1-7), 2(1, 1-2), 3(1, 1-2), 4(2, 1-4), 5(1, 1-2), 6(1, 1-2), 7(1, 1-2) present in some, 9(1), 10(1, present in some), 11(1-2, present in some). Segment III: hair 0(1), 1(3, 1-5), 2(1, 1-3), 3(1, 1-2), 4(2, 1-3), 5(1, 1-2), 6(1), 7(2, 1-3), 8(3, 2-4), 9(1), 10(1, 1-3), 11(1), 14(1). Segment IV: hair 0(1), 1(2, 2-5), 2(1), 3(2, 2-4), 4(2, 1-2), 5(2), 6(1), 7(2, 1-2), 8(2, 1-3), 9(1), 10(1), 11(1), 14(1). Segment V: hair 0(1), 1(2, 1-3), 2(1, 1-2), 3(1, 1-3), 4(1, 1-3), 5(2), 6(1), 7(2, 1-4), 8(2, 1-3), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1, 1-2), 5(1, 1-2), 6(1), 7(1, 1-2), 8(2, 1-2), 9(1), 10(1, 1-2), 11(1), 14(1). Segment VII: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1), 5(1, 1-3), 6(2, 1-3), 7(1), 8(3, 1-4), 9(4, 2-5), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(6, 4-9), 14(1). *Paddle*: Uniformly moderately pigmented, midrib darker; external margin serrated, apex smooth; hair 1-X slender. Male genital lobe extending to 0.59 of paddle, female genital lobe to 0.41.

LARVA (fig.44). Head: 0.76 mm. Siphon: 0.65 mm. Anal Saddle: 0.27 mm. Chaetotaxy as given below, hairs moderately to darkly pigmented. *Head*: Mental plate with a strong median tooth and 9-11 distinct teeth on either side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(7, 4-8), 5(1, strong), 6(3, 2-3), 7(3, 2-3), 8(1), 9(2, 2-3), 10(2, 1-2), 11(17, 10-19, stellate), 12(1), 13(1), 14(12, 12-24, stellate), 15(2, 2-4). *Antenna*: Length about 0.3 of head; pigmentation moderate; shaft with a few scattered denticles. All hairs except 1-A single; hair 1-A (2, 2-3) about 0.6 from base. *Thorax*: Integument strongly pilose, spicules simple, hairlike; apices of long hairs attenuate and weakly barbed. Stellate hairs with many barbed branches. Prothorax: hair 0(23, 19-25), 1(5, 2-8), 2(1, 1-2), 3(20, 18-26), 4(1, 1-3), 5(1), 6(1), 7(2, 2-3), 8(20, 15-23), 9(17, 16-24), 10(1), 11(1, 1-2), 12(1), 13(20, 18-29), 14(32, 30-42). Mesothorax: hair 1(11, 8-15), 2(1), 3(1), 4(1), 5(1), 6(4, 3-5), 7(1), 8(5, 4-6), 9(5, 4-6), 10(1), 11(2, 1-4), 12(1, 1-2), 13(17, 12-21), 14(16, 10-20). Metathorax: hair 1(21, 9-21), 2(1), 3(8, 3-9), 4(13, 12-18), 5(11, 9-16), 6(1), 7(4, 3-5), 8(17, 12-19), 9(3, 2-5), 10(1), 11(2, 2-4), 12(1), 13(22, 16-26). *Abdomen*: Integument and stellate hairs as on thorax. Spicules as on thorax, but longer and more profuse on ventral side of segments. Segment I: hair 1(20, 12-21), 2(20, 18-25), 3(1), 4(1), 5(15, 13-20), 6(2, 2-3), 7(1), 9(7, 5-10), 10(1), 11(20, 12-23), 13(15, 9-16). Segment II: hair 0(1), 1(20, 16-26), 2(20, 16-24), 3(1), 4(1, 1-2), 5(16, 12-17), 6(2, 2-3), 7(9, 5-11), 8(1), 9(10, 6-13), 10(1, 1-2), 11(1, 1-2), 12(1), 13(14, 12-18). Segment III: hair 0(1), 1(20, 16-23), 2(20, 9-24), 3(1), 4(1), 5(14, 14-20), 6(2), 7(14, 11-17), 8(1), 9(14, 10-18), 10(1), 11(1), 12(1), 13(13, 11-17), 14(1). Segment IV: hair 0(1), 1(20, 12-21), 2(22, 13-25), 3(1), 4(1), 5(15, 12-20), 6(2), 7(13, 10-15), 8(1), 9(18, 11-19), 10(1), 11(1), 12(1), 13(11, 9-17), 14(1). Segment V: hair 0(1), 1(17, 12-21), 2(18, 17-24), 3(1), 4(1), 5(15, 13-20), 6(2), 7(12, 10-15), 8(1), 9(16, 13-19), 10(1), 11(1), 12(1), 13(10, 9-14), 14(1). Segment VI: hair 0(1), 1(17, 12-20), 2(18, 17-22), 3(1), 4(1), 5(16, 13-17), 6(1, 1-2), 7(11, 8-12), 8(1), 9(17, 11-19), 10(1), 11(1), 12(1), 13(12, 8-15), 14(1). Segment VII: hair 0(1), 1(18, 12-18), 2(18, 15-21), 3(1), 4(1), 5(13, 11-17), 6(8, 8-12), 7(1), 8(9, 8-10), 9(12, 12-21), 10(1), 11(1), 12(1), 13(9, 7-12), 14(1). *Segment VIII*: Comb scales in a single row, usually 10(8-14) in number;

individual scale long, pointed apically and fringed nearly to tip. Hair 0(1), 1(20, 17-24), 2(1), 3(7, 5-8), 4(1), 5(15, 12-17), 14(1). *Siphon*: Index about 2.1-2.4; integument moderately pigmented, imbricate. Pecten extending to 0.42-0.45, with 13-20 teeth; individual tooth long, pointed, with basal denticles. Hair 1(2, 2-3), 2(1), 3-5 not visible, 6(1), 7(1), 8(1, 1-2), 9(1). *Anal Segment*: Saddle moderately pigmented and weakly spiculate; caudal margin with spines of varying length. Gills moderate, about 1.5-2.0 of saddle length, ventral slightly shorter than dorsal. Hair 1(4, 3-5), 2(5, 3-6), 3(2), 4a(3, 2-4), 4b(2, 2-3), 4c(2, 2-3), 4d(2, 2-3), 4e(2, 2-3).

EGG. Length about 0.73 mm, width 0.1 mm; exochorion transparent, with circular clear refractile bodies; endochorion dark, with irregular polygonal sculpturing.

SYSTEMATICS. Formerly the name *sexlineatus* was applied to quite unrelated forms, some of which are now recognized as distinct species in other groups of the *Sexlineatus* Section. In the restricted sense used here, with the diagnostic features mentioned under the group and the species, *sexlineatus* appears to be a complex of several closely related forms. It is impossible at this time to resolve the complex owing to the paucity or total absence of associated immature stages and even adults from critical areas. The best diagnostic features of the complex are: (1) in the adults, the presence of dark scales on the upper *ppn* and antealar area; and (2) in the larvae, the presence of a dense vestiture of hairlike spicules on the thorax and abdomen; the aedeagus of the male genitalia may also prove to be distinctive. I have seen samples from populations with these characters from central and southern Mexico, Honduras, Panama, Ecuador, Venezuela and Trinidad. The species has been reported from intermediate areas but little reliance can be placed on these records although probably the complex does occur throughout Central America and in Colombia.

The description of the species is based on topotypic associated material from Trinidad. The females and 4 males from Venezuela are so similar to those from Trinidad except for slightly yellowish mesonotal lines that there is no question that they belong to the same taxon. No significant departure was noted in the limited material of immature stages from Venezuela. From the original description and illustration it is evident that *dominicii* Rangel and Romero, 1907 from the Rio Anaucó is based on this population and it is therefore synonymized here with *sexlineatus*. The Trinidad and Venezuela populations appear to be confined to the coastal areas and are known from near sea level to moderate elevations in the coastal ranges.

The Ecuador population is known only by males and females from the lowlands of the Guayas River basin. These specimens resemble the typical populations except for fewer dark scales on the upper *ppn* and a tendency toward more extensive light scaling on the tarsi, some specimens showing some white scales on segment 3 of the foretarsus, segments 3 and/or 4 of the midtarsus and segments 4 and/or 5 of the hindtarsus. In the male genitalia, some of the setae of the ninth tergite lobe are slightly flattened, approaching the condition characteristic of *ecuadoriensis* of the Eleonorae Group.

Limited material of all stages has been examined from Panama. While the majority of adults agree with the typical populations, 2 show a preponderance of white scales on the upper *ppn*. I have not been able to detect any significant differences in the immature stages from the typical populations.

The 3 females from Honduras, 2 females from Colombia and all adults from Mexico differ from the typical populations apparently only in the presence of fewer dark scales on the upper *ppn*. In the limited material of immature stages from Mexico no significant differences from typical populations were noted. These populations are found at higher elevations than the typical ones, particularly the ones from Cuerna-

vaca, Mexico (about 7,000 feet).

In the southern portion of the range, populations of *sexlineatus* are apparently largely or entirely restricted to the rain forest and tropical deciduous forest at low and moderate elevations. This may be the case even in Central America and Mexico where *sexlineatus* populations are known only from higher elevations where patches of such forests may be present.

BIONOMICS. Immature stages of *sexlineatus* have been collected only in epiphytic bromeliads. Females are readily attracted to human bait and Trapido and Galindo (1957) found that in Panama they bite both at ground level and in the forest canopy. Attempts at experimental infection with the yellow fever virus have yielded negative results in Trinidad (Aitken 1960:4). Similar negative results have been reported by Boshell-Manrique and Osorno-Mesa (1944:174,177,178) but it is doubtful that the species involved was actually *sexlineatus*.

DISTRIBUTION (fig.4). Mexico (southern part), probably Guatemala, Honduras, Nicaragua, possibly Costa Rica, Panama, Colombia (upper Orinoco drainage), Venezuela (northern), Trinidad and Ecuador (Guayas River basin) at elevations of 250-7000 ft. Material examined: 1099 specimens; 28 ♂, 684 ♀, 35 pupae, 352 larvae; 32 individual rearings (1 pupal, 24 larval, 7 incomplete).

COLOMBIA. *Boyaca*: Cuincha, 2 ♀; Guamales, 2 ♀; San Isidro, 3 ♀ (Boshell-Manrique and Osorno-Mesa 1944:174,177,178). *Meta*: Retiro, 15-16-19 Aug 1935, 2 ♀ [UCLA, USNM].

ECUADOR. Babahoyo, Aug 1938, F. Campos, 4 ♂, 18 ♀ [USNM]; Balzapamba, Aug 1938, F. Campos, 4 ♂, 1 ♀ [USNM], 6 ♀ (KO 209A-21), 1939 or 1941, H. Hansen, 2 ♀ (KO 209A-14) [UCLA]. Guayaquil, J. Murdock, 2 ♂, 3 ♀ [USNM].

HONDURAS. Tegucigalpa, 15 July 1945, 3 ♀ [USNM].

MEXICO. *Chiapas*: San Cristobal (Martini 1935:49). Tuxtla, 23 July 1963, E. Fisher (MF 8), 21 ♀; Sumidero, 17 Aug 1964, D. Verity, 1 lp♂ (117-11), 4 L (MEX 117), 1 lp♂ (118-10); 17 Aug 1964, E. Fisher and D. Verity, 1 ♀ (MEX 120), 1 ♀ (MEX 121), 8 ♀ (MEX 128) [UCLA]. *Morelos*: Cuernavaca, elev. 7000 ft, 29 July 1961, R. and K. Driesbach, 2 ♂, 2 ♀ [USNM]. *Veracruz*: Cordoba, 12 July 1964, E. Fisher and D. Verity, 5 ♀ (MEX 18), 1 ♀ (MEX 19), 1 ♀ (MEX 21); 13 July 1964, E. Fisher and D. Verity, 3 ♀ (MEX 26), 1 lp♂ (28-14), 1 lp♀ (28-11); 16 July 1964, E. Fisher and D. Verity, 1 L (MEX 38) [UCLA].

NICARAGUA. Villa Somoza, Aug, Sept, Nov 1953, 1 ♀ (Galindo and Trapido 1957:146).

PANAMA. *Bocas del Toro*: Almirante, 1952-53, 77 A (Trapido and Galindo 1957:122,125). *Cocle*: El Valle, elev. 2000 ft, 14 Aug 1963, A. Quinonez (PA 533), 1 IP (533-101); Valle de Anton, elev. 2400 ft, 13 Aug 1963, A. Quinonez (PA 504), 3 lp♂ (504-101,102,108), 1 lp♀ (504-104), 1 p♂ (504-103), 1 IP (504-106) [UCLA]. Tucue, elev. 1000 ft, 12 June-14 Dec 1950, 2 A (Trapido, Galindo and Carpenter 1955:530). *Panama*: Campana, elev. 2000 ft, 14 June-6 Dec 1950, 24 A (Trapido, Galindo and Carpenter 1955:530).

TRINIDAD. *Caroni*: Brasso Venado, elev. 400 ft, 21 June 1964, R.L. Manuel and R. Martinez, 24 ♀ (TR 513) [UCLA]. *Mayaro*: Bush Bush Forest, 9 Dec 1963, TRVL, 2 ♀ (TR 62); 20 Dec 1963, TRVL, 1 ♀ (TR 5); 27 Dec 1963, TRVL, 6 ♀ (TR 21); 30 Dec 1963, TRVL, 2 ♀ (TR 10); 17 Jan 1964, TRVL, 4 ♀ (TR 28); 22 Jan 1964, TRVL, 1 ♀ (TR 40) [UCLA]. *Nariva*: Archers Estate, 5 Nov 1964, A. Guerra, 1 ♀ (TR 819) [UCLA]. Biche, elev. 250 ft, 9 July 1964, F. Powdhar, 3 ♀ (TR 563) [UCLA]. Charuma Forest, elev. 500 ft, 27 Aug 1964, A. Guerra, 24 ♀ (TR 644); 8 Oct 1964, A. Guerra, 3 ♀ (TR 761) [UCLA]. *St. Andrew*: Caratal Road, elev. 250 ft, 3 Dec 1964, F. Powdhar, 1 ♀ (TR 866) [UCLA]. Coryal, elev. 250 ft, 18 June 1964, A. Guerra, 2 ♀ (TR 498) [UCLA]. Mt. Harris, 23-31 July 1924, C.L. Withycombe, 1 ♀ [USNM]; elev. 250 ft, 16 July 1964, F. Powdhar, 16 ♀ (TR 573) [UCLA]. Nestor Village, elev. 100 ft, 12 June 1965, A. Guerra, 1 ♀ (TR 484) [UCLA]. Tamana, 1945, 1 ♀ [USNM]; Mt. Tamana, elev. 250 ft, 19 June 1964, A. Guerra, 43 ♀ (TR 512); 20 Aug 1964, A. Guerra, 1 ♀ (TR 619); elev. 1000 ft, 23 Aug 1964, R.L. Manuel and R. Martinez, 5 ♀ (TR 620) [UCLA]. Valencia, Cumaca, elev. 1000 ft, 3 Sept 1964, A. Guerra, 2 ♀ (TR 654); El Quemado Road, elev. 250 ft, 3 July 1964, F. Powdhar, 1 ♀ (TR 547) [UCLA]. *St. David*: Sans Souci, elev. 250 ft, 5 Mar 1964, A. Guerra, 1 ♀ (TR 151) [UCLA]. *St.*

George: Aripo Valley, elev. 500 ft, 16 Apr 1964, A. Guerra, 1 ♀ (TR 330) [UCLA]. Blanchisseuse, 2 Aug 1945, 18 ♀; 2 Sept 1945, 1 ♀ [USNM]; 1 ♀ (KO 209A-36) [UCLA]; road to Blanchisseuse, 2 Mar 1945, 2 ♀ [USNM]. Guanapo Valley, elev. 1500 ft, 17 Apr 1964, A. Guerra, 1 ♀ (TR 339) [UCLA]. Heights of Guanapo, elev. 800 ft, 26 Mar 1964, A. Guerra, 1 ♀ (TR 259); elev. 1000 ft, 22 Apr 1965, A. Guerra, 63 ♀ (TR 1129) [UCLA]. La Laja Road, elev. 1000 ft, 11 Mar 1965, A. Guerra, 44 ♀ (TR 1036) [UCLA]. La Laja Trace, 11 Mar 1965, 2 lp♂ (1041-22,41), 1 lp♀ (1041-18), 2 lp (1041-21,23), 2 P, 33 L, 13 1 [UCLA]. Las Lapas Trace, elev. 2000 ft, 3 Apr 1964, A. Guerra, 12 ♀ (TR 281) [UCLA]. Mt. Beck, elev. 1000 ft, 29 Apr 1965, A. Guerra, 1 ♀ (TR 1132) [UCLA]. Port of Spain, 26 Aug 1945, 1 ♀ [USNM]. Simla, 25 Mar 1965, M.J. Moody, 6 ♀ (TRM 15) [UCLA]. Springhill Estate, elev. 1200 ft, 25 Mar 1965, A. Guerra and M.J. Moody (TRM 12), 2 lp♀ (12-50,52), 10 L; 25 Mar 1965, A. Guerra, 2 lp♀ (1056-11,14), 1 P, 5 L, 1 1 (TR 1056), 3 lp♀ (1063-31,81,82), 6 ♀, 86 L (TR 1063), 2 lp♂ (1064-11,12), 1 ♀, 3 L (TR 1064) [UCLA]. Verdant Vale, elev. 1000 ft, 10 Sept 1964, A. Guerra, 5 ♀ (TR 686); elev. 500 ft, 12 Nov 1964, A. Guerra, 21 ♀ (TR 831); 9 Apr 1965, elev. 1200 ft, A. Guerra, 3 ♀, 132 L (TR 1098), 1 lp♂ (1099-33), 3 lp♀ (1099-11,21,22), 3 1P (1099-12,31,32), 34 L [UCLA]. *County not specified*: June 1905, A. Busck, 15 ♀; A. Busck, 7 ♀; F.W. Urich, 1 ♀ [USNM].

VENEZUELA. *Anzoategui*: Puerto La Cruz, Sept 1944, W.H.W. Komp, 1 ♀ (KO 209A-15), 2 ♂ (KO 209A-20); 26 Sept 1944, W.H.W. Komp, 10 ♀ (KO 209A-24), 23 ♀ (KO 209A-27), 24 A (KO 209A-35) [UCLA]. *Aragua*: Guamitas, elev. 1200 m, 27 Jan 1927, M.N. Tovar, 3 ♀; 24 Aug 1927, M.N. Tovar, 136 ♀; 27 Aug 1927, M.N. Tovar, 1 ♀ [USNM]. La Providencia (Cova Garcia, Sutil and Rausseo 1966b:74). Maracay, 2 July 1927, M.N. Tovar, 2 ♀; M.N. Tovar, 1 ♀ [USNM]. Rancho Grande, 2 Nov 1962, I. Ortiz C., 7 ♀ [USNM]. Turmero (Cova Garcia, Sutil and Rausseo 1966b:74). *Distrito Federal*: Caracas, 21 July 1938, 1 ♂; P.J. Anduze, 1 ♂, 1 ♀ [USNM]; Hacienda El Paraiso, ♀ (Rangel and Romero-Sierra 1907). Carayaca (Cova Garcia, Sutil and Rausseo 1966b:74). *Miranda*: El Hatillo (Cova Garcia, Sutil and Rausseo 1966b:74). *Monagas*: Guacharo, F.M. Root, 5 ♀ (VZR 267) [UCLA].

Whitmorei Group

FEMALES. *Head*: Median light line on vertex with moderately broad scales. Proboscis subequal to forefemur in length. Torus with an almost complete ring of white scales broken only dorsally. *Thorax*: Mesonotal light lines usually white to silvery; inner dorsocentral line complete; outer dorsocentral line shorter, not reaching anterior margin, diverging outwards anteriorly; lateral marginal line broken into narrow prescutal, antealar and supraalar patches; scales on anterior promontory white. Antealar area above paratergite with dark scales. Paratergite and *ppn* with restricted light patch confined to posterior half; upper *stp* patch narrow, elongate. *Legs*: Distal white spot on anterior surface of midfemur present, absent on hindfemur. Tibiae predominantly dark, with light lines or scattered scales. *Wing*: Veins entirely dark scaled. *Abdomen*: Basomedian tergal light markings absent.

MALES. Palpus predominantly dark, white scales restricted to base of segments 4 and 5.

MALE GENITALIA. Lobe of tergite IX prominent, with a few (5-7) strong or many (about 12) weak bristles. Sidepieces separated at base by a distance greater than width of aedeagus; tergomesal and/or sternomesal margins with more or less distinct median lobes. Claspette completely absent. Aedeagus moderate to long, shorter than or subequal to proctiger; apex deeply emarginate, with distinct apical horns.

PUPA (*whitmorei* only). *Cephalothorax*: Trumpets short, index about 3.0, not expanded apically; hair 10-C branched, 12-C single or double. *Abdomen*: Hair 5-IV-V moderate, not exceeding apex of second tergite following; hair 9-VII moderate,

branched, exceeding lateral angle of tergite. *Paddle*: Moderate; apex rounded.

LARVA (*whitmorei* only). *Head*: Hairs 4-7-C moderately pigmented, all at least 5-branched; hair 15-C moderate, exceeding apex of mental plate. *Thorax*: Squarish in outline; integument strongly spiculate, spicules hairlike, simple. *Abdomen*: Integument strongly uniformly spiculate. Hair 8-VII slightly cephalodorsad of 9-VII. *Siphon*: Integument distinctly spiculate; acus distinct, attached. *Anal Segment*: Hair 3-X single; ventral brush with 5 pairs of hairs.

DISCUSSION. The Whitmorei Group of 2 species is the subgenus *Soperia* of authors, which is based on a misidentified species (see discussion under subgenus *Howardina*). This group is a very distinct one in adult ornamentation and male genitalia but is obviously related to other groups in the Sexlineatus Section. Its closest affinities seem to be with the Sexlineatus and Allotecnion Groups. The immature stages of *whitmorei* are less differentiated from other groups of the Sexlineatus Section than are those of *walkeri* from other groups of the Walkeri Section.

The Whitmorei Group is known at present only from Colombia, Venezuela, Bolivia and probably Argentina (fig.5). Although *whitmorei* and *pseudodominicii* have been found together in Meta, Colombia, the 2 species may be largely allopatric, *whitmorei* occupying the northern part of the range of the group. *A. pseudodominicii* penetrates into the Amazon basin at an elevation of less than 2,000 feet in Chimore, Bolivia and apparently into the La Plata basin at moderate elevations in northern Argentina. It is also possible that this group is represented on the eastern slope of the Andes in Ecuador (Levi-Castillo 1953:40).

22. *Aedes* (*Howardina*) *whitmorei* Dunn

Figs.5,9,45,46

1918. *Aedes whitmorei* Dunn, 1918:128-130. TYPE: Lectotype ♀, near emerald mines, Muzo, Colombia, 1916, E.R. Whitmore [USNM; selection of Stone and Knight 1956:226].

Aedes (*Howardina*) *whitmorei* of Bonne and Bonne-Wepster (1925:375); Dyar (1928:230); Edwards (1932:156); Horsfall (1955:471).

Aedes (*Soperia*) *whitmorei* of Lane (1939:98); Anduze (1941:14; 1943:193; 1947:357); Lane (1953:701-703); Reyes (1955:74,89); Stone and Knight (1956:226); Stone, Knight and Starcke (1959:173); Belkin, Schick and Heinemann (1965:9); Forattini (1965:405); Cova Garcia, Sutil and Rausseo (1966a:57,275; 1966b:80-81,141,339).

Aedes whitmorei of Antunes (1937b:77); Senevet and Quievreux (1941:258); Boshell-Manrique and Osorno-Mesa (1944:173,174,175,177,178).

Aedes (*Soperia*) *dominicii* of Komp (1936a:63; 1936b:73-74).

Aedes dominicii in part of Bates (1944:165,166; 1945:23; 1949:16,61,320); Bugher, Boshell-Manrique et al (1944:33,37).

FEMALE. Wing: 2.7 mm. Proboscis: 1.98 mm. Forefemur: 1.98 mm. Abdomen: about 2.4 mm. *Head*: Light decumbent scales on vertex silvery white. Erect scales light on occiput, darkened on sides. Palpus about 0.16 of proboscis, with silvery white scales on apex of segment 4. Torus with silvery white scales. *Thorax* (fig.9): Mesonotal light lines white; inner dorsocentral line very narrow; outer dorsocentral line narrow but with a distinct broad silvery spot of broad scales at anterior end in fossa; lateral marginal line broken into lateral prescutal line, a small antealar and a larger supraalar patches, lateral prescutal nearly continuous but apparently broken at level of humeral bristle. Median scutellar lobe laterally with broad dark scales and

with median broad silvery white scales from base to apex; lateral lobes with a few narrow silvery white scales. Scales on paratergite broad, silvery. Pleural scales broad and silvery; lower *ppn* patch adjoining upper *ssp*; other patches as in the group. *Legs*: Forefemur predominantly dark on both sides except for narrow white longitudinal line posteriorly; midfemur dark anteriorly except for a silvery spot at distal 0.67, proximal 0.5 of posterior surface white, rest dark; hindfemur predominantly white anteriorly to 0.67, distal part dark, proximal 0.5 of posterior surface white, distal dark. Tibiae usually dark, a few whitish scales at base. Foretarsus and midtarsus with short incomplete white rings on segments 1,2; hindtarsus with moderately broad ones on 1-3. *Haltere*: Stem pale, knob predominantly dark, fringe scales whitish. *Abdomen*: Basomedian tergal pure white scales evident on segments V-VII. Sternites with broad basal V-shaped pure white patches; apical light scales inconspicuous.

MALE. Wing: 2.5 mm. Proboscis: 2.34 mm. Forefemur: 1.89 mm. Essentially similar to female in color; only apparent difference is a small ventromedian white spot on the proboscis.

MALE GENITALIA (fig.45). As figured; diagnostic characters as in the key. Ninth tergite lobe prominent, with 6,7 moderately strong bristles. Sidepiece rather short, length about 2.0 of median width; tergomesal margin with a row of unpigmented leaflike setae, sternomesal lobe with a dense tuft of pigmented leaflike setae on an elevated flap. Clasper about 0.5 of sidepiece, with spicules in basomesal area; spiniform moderately long, about 0.35 of clasper length. Aedeagus narrow, subequal to proctiger, apex deeply emarginate, with distinct horns curved laterally.

PUPA (fig.45). Abdomen: 2.86 mm. Trumpet: 0.32 mm; index about 3.0. Paddle: 0.67 mm. Diagnostic characters as in the key. Chaetotaxy as given below, hairs moderately pigmented. *Cephalothorax*: Mesonotum lightly pigmented between trumpets, lateral areas slightly darker; metanotum uniformly moderately pigmented. Trumpets short, strongly pigmented and contrasting. Hair 1(1), 2(1), 3(1), 4(3, 2-4), 5(2), 6(1), 7(2), 8(1, 1-3), 9(1, 1-2), 10(4, 2-5), 11(1), 12(2, 1-2). *Abdomen*: Tergite I uniformly lightly pigmented, except for usual membranous areas; rest of segments imbricate and lightly pigmented, progressively lighter caudad. Segment I: hair 1(7-12 primary branches, each with few secondary ones), 2(1), 3(1), 4(2, 2-3), 5(1, 1-3), 6(1), 7(1), 9(1), 10(1, present in a few), 11(2, 1-4, present in a few). Segment II: hair 0(1), 1(4, 2-5), 2(1), 3(1), 4(2, 2-3), 5(1, 1-2), 6(1), 7(1, 1-2), 8(1), 9(1), 10(1). Segment III: hair 0(1), 1(3, 2-5), 2(1), 3(1), 4(1, 1-2), 5(1, 1-2), 6(1), 7(2, 1-3), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment IV: hair 0(1), 1(2, 2-4), 2(1), 3(2, 2-3), 4(1), 5(2), 6(1), 7(2, 2-4), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment V: hair 0(1), 1(2, 2-3), 2(1), 3(1), 4(2, 1-4), 5(1), 6(1), 7(2, 2-5), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(1, 1-3), 2(1), 3(1), 4(1, 1-2), 5(2), 6(1), 7(1, 1-3), 8(1, 1-2), 9(1), 10(1, 1-2), 11(1), 14(1). Segment VII: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1), 5(1), 6(2, 2-3), 7(1), 8(3, 3-4), 9(5, 4-6), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(10, 8-11), 14(1, 1-2). *Paddle*: Uniformly lightly pigmented, midrib slightly darker; external margin serrated. Male genital lobe extending to 0.5 of paddle, female genital lobe to 0.39.

LARVA (fig.46). Head: 0.84 mm. Siphon: 0.81 mm. Anal Saddle: about 0.3 mm. Diagnostic characters as in the key. *Head*: Width subequal to length; pigmentation moderate except around mouthparts where it is deeper. Mental plate with a strong median tooth and 11 distinct teeth on each side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(15, 10-16), 5(6, 5-8), 6(7, 6-7), 7(14, 11-17), 8(3, 3-6), 9(11, 8-14), 10(1), 11(20, 16-20), 12(5, 4-7), 13(1), 14(14, 11-14), 15(3, 2-3). *Antenna*: Length about 0.32 of head; shaft rather uniformly pigmented and with a few

scattered spicules; hair 1(3, 2-3), other single. *Thorax*: Stellate hairs with many unequal, weakly barbed branches; long hairs attenuate apically and weakly barbed. *Prothorax*: hair 0(19, 19-23), 1(5, 4-6), 2(1), 3(21, 13-23), 4(1), 5(1), 6(1), 7(2), 8(20, 16-20), 9(14, 14-17), 10(1), 11(1), 12(1), 13(22, 20-25), 14(34-51). *Mesothorax*: hair 1(14, 13-20), 2(1), 3(1), 4(1), 5(1), 6(5, 4-6), 7(1), 8(6, 6-7), 9(5, 4-6), 10(1), 11(2, 1-3), 12(1), 13(17, 10-19), 14(16, 16-21). *Metathorax*: hair 1(25, 20-27), 2(1), 3(2, 1-2), 4(18, 17-19), 5(18, 17-23), 6(1), 7(5, 4-6), 8(18, 16-22), 9(4, 3-6), 10(1), 11(2, 1-2), 12(1), 13(22, 19-24). *Abdomen*: Integument and stellate hairs as on thorax. *Segment I*: hair 1(23, 20-25), 2(20, 20-25), 3(1), 4(1), 5(16, 14-23), 6(2, 2-3), 7(1), 9(8, 7-8), 10(1), 11(18, 15-20), 13(22, 22-25). *Segment II*: hair 0(1), 1(21, 20-24), 2(22, 18-25), 3(1), 4(1), 5(24, 18-24), 6(2, 2-3), 7(10, 9-10), 8(1), 9(14, 9-15), 10(1), 11(1), 12(1), 13(20, 19-24). *Segment III*: hair 0(1), 1(22, 19-25), 2(21, 18-27), 3(1), 4(1), 5(19, 17-26), 6(2), 7(17, 14-20), 8(1), 9(16, 14-21), 10(1), 11(1), 12(1), 13(20, 16-26), 14(1). *Segment IV*: hair 0(1), 1(20, 17-24), 2(22, 20-22), 3(1), 4(1), 5(22, 18-25), 6(2), 7(15, 9-18), 8(1), 9(19, 18-23), 10(1), 11(1), 12(1), 13(18, 14-20), 14(1). *Segment V*: hair 0(1), 1(22, 16-23), 2(19, 17-23), 3(1), 4(1), 5(20, 18-23), 6(2), 7(15, 12-18), 8(1), 9(19, 18-24), 10(1), 11(1), 12(1), 13(19, 16-22), 14(1). *Segment VI*: hair 0(1), 1(19, 19-23), 2(19, 18-23), 3(1), 4(1), 5(21, 18-22), 6(1), 7(11, 10-18), 8(1), 9(20, 17-21), 10(1), 11(1), 12(1), 13(17, 13-18), 14(1, 1-2). *Segment VII*: hair 0(1), 1(20, 18-21), 2(18, 16-22), 3(1), 4(1), 5(16, 16-22), 6(10, 10-13), 7(1), 8(10, 8-11), 9(16, 11-18), 10(1), 11(1), 12(1), 13(11, 10-14), 14(2, 1-2). *Segment VIII*: Comb scales usually 12(9-12) in number, in a single row; individual scale long, pointed apically and fringed almost to tip. Hair 0(1), 1(28, 22-28), 2(1), 3(8, 7-9), 4(1), 5(15, 10-19), 14(2, 2-3). *Siphon*: Index about 3.0, distinctly swollen in middle; integument uniformly moderately to strongly pigmented, with darker basal ring, uniformly spiculate. Pecten teeth usually 16(14-20) in number, extending to 0.4 before hair 1-S. Hair 1(3, 2-3), 2(1), 3-5 not visible, 6(1), 7(1), 8(1, 1-2), 9(1). *Anal Segment*: Saddle strongly pigmented, with darker basal ring; integument uniformly covered with spicules; caudal margin with spines of varying length; gills subequal, long, more than 2.0 of saddle length. Hair 1(2), 2(4, 3-4), 3(1), 4a(2), 4b(2), 4c(2, 1-2), 4d(2, 1-2), 4e(1, 1-2).

SYSTEMATICS. *A. whitmorei* is a very strikingly differentiated species erroneously synonymized with *dominicii* by Komp (1936a:53); the latter as shown here is undoubtedly *sexlineatus* (see). Its only close relative is *pseudodominicii*, whose immature stages are unknown. In ornamentation of the adults and in male genitalia the 2 species are readily separated by the features mentioned in the diagnoses and keys. *A. whitmorei* is known at present from both sides of the Cordillera Oriental in Colombia and from the Cordillera de la Costa in northcentral Venezuela; it probably occurs also in the intermediate areas in the Cordillera de Merida in western Venezuela. On the eastern slope of the Cordillera Oriental *whitmorei* is sympatric with *pseudodominicii* whose distribution extends on down to northern Argentina along the eastern slopes of the Andes.

BIONOMICS. Immature stages of *whitmorei* have been collected in epiphytic bromeliads at elevations of about 3,000 feet. Dunn's (1918:130) record from "small heavily shaded pools of clear but apparently stagnant water" is probably erroneous. According to Bates (1949:16,61), *whitmorei* (as *dominicii*) is a relatively common diurnal forest mosquito in the region of Villavicencio in Colombia; the females bite both at ground level and in tree stations; and males are often observed hovering over men and animals in the forest. Experimental infections of this species (also as *dominicii*) with yellow fever virus have been unsuccessful (Bugher, Boshell-Manrique et al

1944:33,37).

DISTRIBUTION (fig.5). Colombia (upper Orinoco and Magdalena drainages) and Venezuela (Cordillera de Merida and Cordillera de la Costa) at moderate elevations. Material examined: 104 specimens; 32 ♂, 43 ♀, 7 pupae, 22 larvae; 7 individual larval rearings.

COLOMBIA. *Boyaca*: Las Animas, 500 yds from mine, 17 Aug 1916, 6 ♀ [USNM]. Muzo, emerald mines, E.R. Whitmore, 1 ♀; 16 Aug 1916, E.R. Whitmore, 10 ♀, type series [USNM]. Guamales, 51 ♀; Tamborredondo, 1 ♀; Cuincha, 162 ♀; San Isidro, 37 ♀ (Boshell-Manrique and Osorno-Mesa 1944:174,175,177,178). *Meta*: Palucho, 3 ♂, 2 ♀ [USNM]. Restrepo, 17 July 1935, W.H.W. Komp, 1 ♂, 1 ♀ (KO 203A-10); 20 Aug 1935, W.H.W. Komp, 1 ♂ (KO 209A-2) [UCLA]; Aug 1935, W.H.W. Komp, 2 ♂, 3 ♀; 9 Sept 1935, W.H.W. Komp, 1 ♂, 2 ♀, 10 L [USNM], 2 ♂, 3 ♀ (KO 209A-28) [UCLA]; 1935, W.H.W. Komp, 1 ♂ (KO 209A-40), 1 ♂ (KO 209A-42), 1 ♂ (KO 209A-44) [UCLA]; July 1935, 2 ♂; Sept 1935, 2 ♀; 1935, 2 ♂; 4 June 1940, 1 ♂; 2 ♂ [USNM]; Retiro, 22 Aug 1935, W.H.W. Komp, 5 ♂; 15-16-19 Aug 1935, 2 ♀ [USNM]. Villavicencio, Buena Vista, elev. 3000 ft, 9 July 1965, E. Osorno-Mesa et al (COB 68), 1 lp♂ (68-30), 2 L [UCLA]; 4 June 1942, W.H.W. Komp, 2 ♂ [USNM]; Forzosa, 25 Oct 1943, M. Bates, 1 ♀ [USNM]; Quebrada Colorado, elev. 2300 ft, 9 July 1965, E. Osorno-Mesa et al (COB 67), 4 lp♂ (67-20,22,23,25), 2 lp♀ (67-21, 24), 3 L [UCLA].

VENEZUELA. *Aragua*: Ocumare de la Costa, 5 July 1927, M.N. Tovar, 5 ♀ [USNM]. Rancho Grande, 2 Nov 1942, I. Ortiz C., 3 ♀ [USNM]. *Distrito Federal*: Caracas (Anduze 1943:193; Cova Garcia, Sutil and Rausseo 1966b:80). Cementerio (Cova Garcia, Sutil and Rausseo 1966b:81). *Merida*: Bailadores (Cova Garcia, Sutil and Rausseo 1966b:81). Tovar (Anduze 1947:357). *Tachira*: Jaurequi and Uribante (Anduze 1947:357).

23. *Aedes* (Howardina) *pseudodominicii* Komp

Figs.5,9,58

1936. *Aedes pseudodominicii* Komp, 1936a:75. TYPE: Holotype ♂, Restrepo, Meta, Colombia, Aug-Sept 1935, E. Osorno-Mesa [NE].

1955. *Aedes* (*H.*) *delpontei* Martinez and Prosen, 1955:35-40. TYPE: Holotype ♂, Chapare, Cochabamba, Bolivia, elev. 6000 ft, Jan 1949, Feb 1952 or Nov 1953, Martinez and Prosen [MEPRA]. **NEW SYNONYMY.**

Aedes (*Soperia*) *pseudodominicii* of Komp (1936b:63; 1956:37).

Aedes (*Soperia*) *dominicii* of Antunes (1937a:16; 1937b:76-77); Lane (1939:98); Senevet and Quievreux (1941:258); Anduze (1943:192-193); Boshell-Manrique and Osorno-Mesa (1944:173, 174,175,177,178); Levi-Castillo (1952:555; 1953:40); Lane (1953:700-701); Reyes (1955:73, 89); Stone, Knight and Starcke (1959:173); Forattini (1965:405).

Aedes (*Soperia*) *dominicii* in part of Bates (1944:165,166; 1945:23; 1949:16,61,320); Bugher, Boshell-Manrique, et al (1944:33,37).

Aedes (*Howardina*) *dominicii* of Horsfall (1955:471).

Aedes (*H.*) *delpontei* of Martinez and Prosen (1959:603,605); Stone, Knight and Starcke (1959:174); Prosen, Carcavallo and Martinez (1964:104,119).

FEMALE. Wing: 3.42 mm. Proboscis: 2.61 mm. Forefemur: 2.61 mm. Abdomen: about 3.24 mm. Similar to *whitmorei* but usually slightly larger in size and differing in the following. *Head*: Light decumbent scales white. Erect scales on occiput and sides whitish. Palpus about 0.17 of proboscis, with a few mesal and apical white scales on segment 4. Torus scales white. *Thorax* (fig.9): Mesonotal light lines white, rarely faintly creamy; inner and outer dorsocentral line without silvery spot in fossal area. Scutellar light scales white. Pleural scale patches white and distributed as in

whitmorei. *Legs*: Forefemur predominantly auburn except for a few basal white scales anteriorly and a narrow longitudinal line posteriorly; midfemur predominantly auburn except for a white spot at distal 0.67 anteriorly and a mesal white line to middle posteriorly; hindfemur predominantly white on both sides, rest mostly auburn; midfemur and hindfemur with a short mesal patch merging with knee spot. Foretibia predominantly auburn, with a few scattered white scales; midtibia and hindtibia with a continuous white line, rest auburn. Foretarsus with a few white scales on segment 1; midtarsus with short incomplete white ring on 1; hindtarsus with broader white rings on segments 1,2. *Haltere*: Stem brownish, knob predominantly auburn, with a few white fringe scales. *Abdomen*: Basal sternal light scales white, apical white scales apparent to segment V, rest auburn.

MALE. Wing: 2.52 mm. Proboscis: 2.34 mm. Forefemur: 1.9 mm. Essentially similar to female in color. Proboscis completely dark.

MALE GENITALIA (fig.58). As figured; diagnostic characters as in the key. Ninth tergite lobe prominent, with many (about 12) narrow bristles. Sidepiece rather short, broader at the middle, tergomesal area with few and sternomesal area with numerous narrow setae. Clasper about 0.6 of sidepiece, stout, curved; spiniform short. Aedeagus shorter than proctiger; dorsal sclerotization deeply emarginate, apical horns distinct, curved upwards and dorsally.

PUPA, LARVA unknown.

SYSTEMATICS. *A. pseudodominicii* is a distinct, clearly marked species erroneously synonymized by Antunes (1937a:16) with *dominicii*; the latter is actually *sexlineatus* (see). On the basis of ornamentation of the adults (only stages known), *pseudodominicii* is evidently closely related to *whitmorei*, which has also been confused (Komp 1936a:53; 1936b:73-74) with *dominicii*. The 2 species are easily distinguished by the diagnostic features given above. *A. pseudodominicii* apparently occurs at moderate elevations only along the eastern slopes of the Andes, from the Cordillera Oriental in Colombia, where it is sympatric with *whitmorei*, all the way down to northern Argentina. It penetrates the upper reaches of the 3 main eastern drainage systems of South America, the Orinoco, Amazon and La Plata. Although I have not seen any of the type material of *delpontei* Martinez and Prosen, 1955, it is evident that this population from Bolivia is conspecific with the typical population from Colombia as the original description of *delpontei* obviously matches in all pertinent details the diagnostic features of *pseudodominicii* as do 2 females collected by Torres-Munez at the type locality of *delpontei*. I have not seen the female paratype of *delpontei* from Argentina but see no reason to doubt its conspecificity with the material from Bolivia and Colombia.

BIONOMICS. The immature stages of *pseudodominicii* are unknown but undoubtedly will be found in epiphytic and/or terrestrial bromeliads. It is very likely that the reports of Bates (1949) and Bugher and Boshell-Manrique et al (1944) mentioned under *whitmorei* apply at least in part to *pseudodominicii* since at that time both species were probably identified as *dominicii*.

DISTRIBUTION (fig.5). Colombia (upper Orinoco and Magdalena drainages), Bolivia (upper Amazon drainage) and Argentina (upper La Plata drainage) at moderate elevations. Material examined: 20 specimens; 10 ♂, 10 ♀; no individual rearings.

ARGENTINA. *Salta*: Campamento San Pedro S.O.C., Departamento San Martin, 1 ♀ paratype of *delpontei* (Martinez and Prosen 1955:40).

BOLIVIA. *Cochabamba*: Chapare, Chimore, 29 June 1944, Torres-Munoz, 1 ♀; 29 Apr 1944, 1 ♀ [USNM]. *La Paz*: Nor Yungas, A (Prosen, Carcavallo and Martinez 1964:104).

COLOMBIA. *Boyaca*: La Bodega, 22 ♀; Guamales, 58 ♀; Tamborredondo, 33 ♀; Cuincha, 19 ♀;

San Isidro, 15 ♀ (Boshell-Manrique and Osorno-Mesa 1944:173,174,175,177,178). *Meta*: Palucho, 2 ♂ [USNM]. Restrepo, 26 July 1935, W.H.W. Komp, 1 ♀ (KO 209A-39); 20 Aug 1935, W.H.W. Komp, 4 ♂ (KO 209A-2) [UCLA]; 7 Sept 1935, E. Osorno-Mesa, 1 ♂; 1935, W.H.W. Komp, 1 ♂; July 1935, 1 ♀ [USNM]; Retiro, 26 July 1935, W.H.W. Komp, 3 ♀ (KO 209A-31) [UCLA]; 15-19 Aug 1935, 1 ♂, 2 ♀ [USNM]. Villavicencio, Buena Vista, 4 June 1942, W.H.W. Komp, 1 ♂ [USNM].

Allotecnnon Group

FEMALES. *Head*: Median light line on vertex with narrow scales. Proboscis distinctly longer than forefemur. Torus with a restricted mesal scale patch. *Thorax*: Mesonotal light lines golden; inner and outer dorsocentral lines complete, subparallel; lateral marginal line continuous; scales on anterior promontory creamy to golden. Antealar area above paratergite with golden scales. Paratergite with a moderate scale patch extending entire sclerite length. Upper *ppn* entirely covered with light scales; upper *stp* patch narrow, elongate. *Legs*: Distal white spot on anterior surface of mid-femur and hindfemur present. Tibiae completely dark. *Wing*: Veins entirely dark scaled. *Abdomen*: Basomedian tergal light markings present on III-VII.

MALE (*allotecnnon* only). Palpus with basomedian light scales on segments 4 and 5.

MALE GENITALIA (*allotecnnon* only). Lobe of tergite IX not prominent, with 3,4 strong bristles. Sidepieces separated at base by a distance less than width of aedeagus; without any indication of lobes on tergomesal or sternomesal margins. Claspette represented by a conical tubercle. Aedeagus shorter than proctiger; apex shallowly emarginate, lateral lobes inconspicuous.

PUPAE. *Cephalothorax*: Trumpet moderate, index about 6.5, not expanded apically; hairs 10,12-C usually single or double. *Abdomen*: Hair 5-IV-V long, usually exceeding apex of second tergite following; hair 9-VII short, slightly larger than 6, usually not exceeding lateral angle of tergite. *Paddle*: Moderate to long, usually slightly produced on apex.

LARVAE. *Head*: Hair 4-C weak, lightly pigmented, at least 4-branched; 5-C single, moderate, strongly pigmented; 6-C heavy, strongly pigmented, double; 7-C moderate, double or triple; 15-C very short, not extending cephalad of base of mental plate. *Thorax*: Quadrate in outline; integument glabrous. *Abdomen*: Integument covered with small spinelike spicules, restricted to dorsal and ventral surfaces (only ventral in *guerrero*). Hair 8-VII caudolaterad of 9-VII. *Siphon*: Integument imbricate; acus distinct, separate. *Anal Segment*: Hair 3-X double; ventral brush with 5 pairs of hairs.

DISCUSSION. The Allotecnnon Group of 3 species is readily recognized by the unique pleural scale pattern of the adults (particularly the long narrow upper *stp* scale patch) and the short, spinelike spicules on the abdominal segments of the larvae.

The group is known only in Central America and is sympatric with the Quadri-vittatus Group from southern Mexico to central Panama (figs.5,6). *A. allotecnnon*, the only widespread species, occupies primarily the central and southern parts of the range of the group but is also known from Chiapas and the southern end of the Sierra Madre Oriental in Mexico; *guerrero* is apparently endemic to the Sierra Madre del Sur in Mexico; and *guatemala* is known only from 2 collections on the Pacific slope of central Guatemala. The 3 species appear to be allopatric.

24. *Aedes* (Howardina) *allotecnon* Kumm, Komp and Ruiz

Figs. 6, 9, 47, 48

1940. *Aedes* (Howardina) *allotecnon* Kumm, Komp and Ruiz, 1940:417. TYPE: Lectotype ♂ with associated larval skin, Poas Volcano, Costa Rica, elev. 9000 ft, 14 Apr 1933, H.W. Kumm [USNM; selection of Stone and Knight 1956:214].

Aedes (Howardina) *allotecnon* of Kumm and Komp (1941:18-22); Kumm and Zuniga (1942:404); Trapido, Galindo and Carpenter (1955:530,534); Stone and Knight (1956:213); Vargas (1956:22); Stone, Knight and Starcke (1959:173); Belkin, Schick and Heinemann (1965:12); Forattini (1965:399); Stone (1967:208).

FEMALE. Wing: 3.5 mm. Proboscis: 2.71 mm. Forefemur: 2.1 mm. Abdomen: about 3.24 mm. *Head*: Light decumbent scales on median stripe and short orbital line creamy; broad light scales on sides and venter whitish. Erect scales on occiput dark. Palpus about 0.19 of proboscis, with white scales on apex and mesal side of segment 4. *Thorax* (fig.9): Inner and outer dorsocentral lines creamy to pale golden, complete; lateral marginal line short, extending from scutal angle to wingbase, appearing broad due to presence of creamy scales in antealar area above paratergite. Median scutellar lobe with moderately broad dark scales laterally and median creamy to golden narrow scales from base to apex; lateral lobes with a few narrow creamy scales. Paratergite with broad white scales. *Apn* with predominantly broad white scales, some anterior ones narrow, creamy. *Ppn* with large upper patch of narrow creamy scales and small lower patch of broad white scales; *psp* without scales; other scale patches silvery white and distributed as in group. *Legs*: Forefemur predominantly dark anteriorly except for basal creamy scales, posterior surface mostly creamy to middle and with a narrow light line bordered on sides by dark scales extending distally; midfemur mostly dark anteriorly except for basal creamy scales and a silvery spot at distal 0.67, mainly creamy posteriorly, dark scales restricted to distal half; hindfemur creamy anteriorly to 0.67 and dark distally except for a silvery spot at 0.75, creamy posteriorly to proximal 0.5, rest dark. Foretarsus with basal white scales on segment 1; midtarsus with short, incomplete white rings on 1,2; hindtarsus with moderate white rings on 1-3. *Haltere*: Stem pale, knob mainly dark, a few fringe scales whitish. *Abdomen*: Basomedian tergal light scales white from segment III distad. Sternites with broad basal V-shaped patches, creamy at base, silvery on sides; median apical light scales evident to segment IV.

MALE. Wing: 2.62 mm. Proboscis: 2.19 mm. Forefemur: 1.77 mm. Essentially similar to female in color. Mesal light scale patch on torus absent.

MALE GENITALIA (fig.47). As figured; diagnostic characters as in the key. Ninth tergite lobe not prominent, with 3,4 strong setae. Sidepiece length 3.0 of median width. Clasper about 0.6 of sidepiece, with 2 preapical hairs; spiniform short, about 0.25 of clasper. Aedeagus shorter than proctiger; dorsal sclerotization shallowly emarginate, lateral lobes inconspicuous.

PUPA (fig.47). Abdomen: 3.08 mm. Trumpet: 0.43 mm; index 6.5. Paddle: 0.7 mm. Diagnostic characters as in the key. Chaetotaxy as given below; hairs moderately to darkly pigmented. *Cephalothorax*: Mesonotum moderately pigmented between trumpets, lateral areas and metanotum slightly darker; trumpets contrasting. Hair 1(1), 2(1, 1-2), 3(1, 1-2), 4(2, 2-4), 5(2), 6(1, 1-2), 7(2), 8(1, 1-3), 9(1), 10(1, 1-4), 11(1), 12(2, 1-2). *Abdomen*: Tergite I deeply pigmented, except for usual membranous areas; tergites II and III deeply pigmented, other segments lighter. Segment I:

hair 1(5-13 primary branches, each with many secondary ones), 2(1, 1-2), 3(1, 1-2), 4(3, 2-5), 5(1, 1-2), 6(1, 1-2), 7(1, 1-2), 9(1), alveoli of 10,11 present in some. Segment II: hair 0(1), 1(3, 2-6), 2(1), 3(1, 1-2), 4(3, 2-5), 5(1), 6(1, 1-2), 7(1, 1-2), 8(1, present in a few), 9(1). Segment III: hair 0(1), 1(3, 2-4), 2(1), 3(1), 4(1, 1-2), 5(1), 6(1), 7(2, 1-4), 8(1, 1-3), 9(1), 10(1), 11(1), 14(1). Segment IV: hair 0(1), 1(2, 2-3), 2(1), 3(2, 1-4), 4(1), 5(2, 1-3), 6(1), 7(2, 1-4), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment V: hair 0(1), 1(2, 1-3), 2(1), 3(1), 4(2, 1-3), 5(2, 1-2), 6(1), 7(2, 2-4), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1), 5(1, 1-2), 6(1), 7(1, 1-2), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1, 1-2), 4(1, 1-4), 5(1, 1-2), 6(2, 1-4), 7(1), 8(2, 1-3), 9(3, 2-7), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(3, 3-5), 14(1). *Paddle*: Uniformly lightly pigmented, midrib darker; external margin serrated; hair 1-P slender. Male genital lobe extending to about 0.4 of paddle, female genital lobe to 0.35.

LARVA (fig.48). Head: 0.84 mm. Siphon: 1.00 mm. Anal Saddle: 0.32 mm. Readily separated from *guerrero* by the presence of abdominal spicules on both dorsal and ventral surfaces and anal saddle with distinct large marginal spicules ventrad of hair 1-X. *Head*: Width about 1.06 of length. Pigmentation moderate except around mouthparts where it is deeper. Mental plate with a strong median tooth and usually 11(11,12) distinct teeth on either side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(5, 4-8), 5(1), 6(2), 7(3, 2-3), 8(1), 9(3, 3-5), 10(2, 1-3), 11(12, 9-17), 12(1, 1-2), 13(1, 1-2), 14(8, 4-9), 15(2, 2-3). *Antenna*: Length about 0.37 of head. Pigmentation moderate; shaft with a few scattered spicules. All hairs except 1, single; hair 1-A (2, 2-4) at about 0.63 from base. *Thorax*: Apices of long hairs attenuate; barbs present on both long and stellate hairs. Prothorax: hair 0(24, 17-29), 1(6, 4-7), 2(1), 3(16, 11-19), 4(2, 1-2), 5(3, 2-3), 6(1), 7(3, 2-4), 8(28, 24-30), 9(28, 22-28), 10(1), 11(2, 2-4), 12(1), 13(33, 22-35), 14(30, 24-38). Mesothorax: hair 1(11, 6-14), 2(1), 3(1), 4(1), 5(1), 6(6, 4-7), 7(1), 8(6, 5-6), 9(7, 5-8), 10(1), 11(2, 1-2), 12(1), 13(16, 10-17), 14(8, 8-13). Metathorax: hair 1(16, 12-25), 2(1), 3(5, 4-9), 4(17, 13-20), 5(15, 13-20), 6(1), 7(6, 3-8), 8(11, 10-14), 9(4, 3-6), 10(1), 11(1, 1-2), 12(1), 13(27, 20-33). *Abdomen*: Integument of segment I glabrous; other segments with spinelike spicules on dorsal and ventral surfaces. Stellate hairs with branches of unequal length. Segment I: hair 1(19, 12-20), 2(28, 17-28), 3(1), 4(6, 4-8), 5(16, 12-19), 6(3, 2-3), 7(1, 1-2), 9(6, 5-9), 10(1), 11(17, 13-21), 13(10, 8-10). Segment II: hair 0(1), 1(17, 11-20), 2(26, 17-26), 3(1), 4(6, 4-8), 5(16, 14-20), 6(3, 2-3), 7(9, 6-11), 8(1, 1-3), 9(6, 4-9), 10(1), 11(1), 12(1), 13(9, 7-16). Segment III: hair 0(1), 1(18, 8-22), 2(24, 16-27), 3(1), 4(1), 5(17, 12-26), 6(2, 2-3), 7(9, 6-12), 8(1), 9(14, 10-18), 10(1), 11(1), 12(1), 13(6, 5-12), 14(1). Segment IV: hair 0(1), 1(14, 5-18), 2(23, 15-27), 3(1, 1-2), 4(1), 5(15, 10-20), 6(2, 2-3), 7(9, 6-13), 8(1), 9(16, 12-22), 10(1), 11(1), 12(1), 13(7, 4-12), 14(1). Segment V: hair 0(1, 1-2), 1(12, 5-15), 2(19, 15-25), 3(1), 4(1, 1-3), 5(15, 11-18), 6(2), 7(8, 6-11), 8(1), 9(16, 11-23), 10(1), 11(1), 12(1), 13(8, 4-10), 14(1). Segment VI: hair 0(1), 1(14, 6-15), 2(17, 13-24), 3(1), 4(1), 5(12, 10-19), 6(2, 2-3), 7(8, 6-11), 8(1), 9(14, 11-17), 10(1), 11(1), 12(1), 13(8, 4-10), 14(1, 1-2). Segment VII: hair 0(1), 1(11, 6-16), 2(16, 11-20), 3(1), 4(1), 5(11, 8-17), 6(9, 6-14), 7(1), 8(5, 3-7), 9(13, 10-21), 10(1), 11(1), 12(1), 13(7, 3-14), 14(1, 1-3). *Segment VIII*: Comb scales in a single row, usually 14(12-20) in number; individual scale elongate, pointed apically and evenly fringed nearly to tip. Hair 0(1), 1(10, 8-20), 2(1), 3(5, 4-6), 4(1), 5(6, 4-8), 14(2, 1-4). *Siphon*: Index about 4.0-4.2; integument moderately pigmented, imbricate. Pecten extending to about 0.55, with 22(17-24) teeth; individual tooth pointed apically, with basal denticles. Hair 1(3, 2-3), 2(1), 3-5 not visible, 6(1), 7(1), 8(1), 9(1). *Anal Segment*: Sad-

dle imbricate; moderately pigmented, with darker basal ring; caudal margin with spines of varying sizes dorsad and ventrad of hair 1-X. Gills subequal, about 2.0 of saddle length. Hair 1(3, 2-4), 2(4, 3-5), 3(2), 4a(4, 2-4), 4b(3, 3-4), 4c(4, 3-4), 4d(3, 2-4), 4e(2, 2-3).

SYSTEMATICS. *A. allotecnon* is the most widespread and most common of the 3 allopatric species in the Allotecnon Group. Its known range extends from the southern end of the Sierra Madre Oriental in Mexico to central Panama. The only significant variation noted in the large series of specimens was the presence of a few silvery scales on upper *ppn* in the 2 females from Mexico (MEX 14,16). Although this condition tends toward *guerrero* the 2 forms appear to be distinct in other adult features and the 3 larvae of *allotecnon* from Mexico are clearly different from those of *guerrero* and apparently indistinguishable from those of *allotecnon* populations in Central America. Only with additional material of all stages from Mexico will it be possible to determine the taxonomic status of this population and its relation to *guerrero*. The distribution of *allotecnon* appears to be discontinuous in Central America probably because of its apparent restriction to areas of cloud forest. Although not reported as yet from Guatemala and Honduras, it may occur there in suitable environments.

BIONOMICS. The immature stages of *allotecnon* have been collected in epiphytic bromeliads at elevations above 5,000 feet, frequently in association with members of the Quadrivittatus Group. A few females have been taken in daytime biting-landing collections on human bait.

DISTRIBUTION (fig.6). Cordilleras of Middle America in Mexico (Sierra Madre Oriental and Sierra Madre de Chiapas), possibly eastern Guatemala, El Salvador, probably Honduras, Nicaragua, Costa Rica and Panama (to Canal Zone) at elevations above 5000 ft. Material examined: 521 specimens; 43 ♂, 48 ♀, 136 pupae, 294 larvae; 114 individual rearings (24 pupal, 46 larval, 44 incomplete).

COSTA RICA. *Alajuela*: Poasito, 14 Nov 1962, C.L. Hogue and W.A. Powder (CR 23), 5 lp♀ (23-101,102,104,106,110), 1 p♂ (23-111), 2 p♀ (23-112,113), 3 IP (23-103,107,108), 6 P, 6 p, 7 L, 1 I [UCLA]. Volcan Poas, 14 Apr 1938, H.W. Kumm, 1 ♂; 1 L, 4 I [USNM]; Summit, 14 Nov 1962, C.L. Hogue and W.A. Powder, 1 lp♂ (20-110), 1 lp♀ (20-109), 6 IP (20-102-106,108), 5 L (CR 20), 2 lp♂ (21-103,106), 2 lp♀ (21-109,110), 1 p♂ (21-112), 1 p♀ (21-101), 6 IP (21-102,104,105,107,109,111), 25 L (CR 21); 9 July 1963, C.L. Hogue, 3 ♂, 2 ♀, 4 P, 4 p, 4 L, 4 I (CR 145) [UCLA]. *Cartago*: Cervantes, 9 Nov 1962, J.N. Belkin, C.L. Hogue and W.A. Powder, 1 L (CR 9), 3 IP (11-101-103), 2 lp♂ (13-104,108), 3 p♂ (13-102,109,110), 3 p♀ (13-101-103), 3 IP (13-103,105,106), 2 L (CR 13), 7 lp♂ (14-102-105,107,111,112), 2 lp♀ (14-109,110), 1 p♂ (14-101), 1 IP (14-108), 2 L (CR 14); 9 Nov 1962, C.L. Hogue (CR 12), 1 lp♂ (12-106), 1 IP (12-105) [UCLA]. La Sierra, elev. 6300-8500 ft, 24 Nov 1962, C.L. Hogue and W.A. Powder, 1 IP (46-201), 1 lp♂ (49-106), 4 lp♀ (49-104,108-110), 4 IP (49-101-103,105), 1 p, 1 L, 1 I (CR 49), 1 p♂ (51-102), 1 p♀ (51-101), 2 IP (51-104,105), 10 L (CR 51), 2 lp♂ (52-101,109), 1 lp♀ (52-104), 4 IP (52-102,103,107,110), 21 L (CR 52), 1 IP (53-104), 1 ♀, 15 L (CR 54) [UCLA]. Orosi, 7 Dec 1962, C.L. Hogue and W.A. Powder (CR 83), 1 lp♀ (83-501), 1 L [UCLA]. Rio Macho, 7 Dec 1962, C.L. Hogue and W.A. Powder, 1 lp♀ (79-102), 1 p♂ (79-101), 2 lp♂ (86-103,104), 1 p♂ (86-101), 1 L (CR 86) [UCLA]. Volcan Irazu, 15 Nov 1962, C.L. Hogue and W.A. Powder (CR 24), 2 p♂ (24-101,108), 1 p♀ (24-106), 3 IP (24-102-104), 1 P, 1 I [UCLA]. *Heredia*: Puerto Viejo, 8 Sept 1965, W.J. Hjort (CR 220), 1 lp♂ (220-11) [UCLA]. *San Jose*: Villa Mills, 21 Nov 1962, C.L. Hogue and W.A. Powder (CR 39), 1 lp♀ (39-104), 3 p♀ (39-101-103), 3 L [UCLA].

EL SALVADOR. Laguna de las Ranas, Jan 1942, H.W. Kumm, 4 ♂, 1 ♀, 2 L [USNM].

MEXICO. *Chiapas*: Sumidero Canyon, 17 Aug 1964, E. Fisher and D. Verity, 3 L (MEX 116), 1 ♀ (MEX 121) [UCLA]. *Veracruz*: Cordoba, Fortin de las Flores, 11 July 1964, E. Fisher, 1 ♀ (MEX 14) [UCLA]. Also from states of *Hidalgo*, *Queretaro* and *San Luis Potosi* (Vargas 1956:22).

NICARAGUA. Jinotega, 3 July 1964, J.N. Belkin and A. Quinonez (NI-33C), 1 IP (33C-41) [UCLA].

PANAMA. *Bocas del Toro*: Chiriquisito, Trail Caldera, 5 Nov 1965, P. Orjuela (PA 1004), 6 ♀ [UCLA]. La Zorra, elev. 4400-5400 ft, 6 Apr 1963, A. Quinonez, 1 L (PA 176); 7 Apr 1963, A. Quinonez, 5 L (PA 179); 8 Apr 1963, A. Quinonez, 4 L, 1 l (PA 180); 9 Apr 1963, A. Quinonez, 7 L (PA 183) [UCLA]. *Chiriqui*: Palo Santo, elev. 4600 ft, 15 June-1 Dec 1950, 1 ♀ (Trapido, Galindo and Carpenter 1955:530). Boquete, 30 Jan 1914, J. Zetek, 1 ♀ [USNM]. El Hato del Volcan, Chiriqui Lagoon, elev. 4500 ft, 12 Mar 1964, A. Quinonez (PA 638), 2 lp♀ (638-101,102), 1 lP (638-108), 1 L [UCLA]. *Cocle*: El Valle, elev. 2000 ft, 24 Aug 1963, A. Quinonez (PA 533), 1 p♀ (533-101), 2 L [UCLA]. *Panama*: Cerro Campana, 3 Aug 1963, A. Quinonez (PA 462), 1 lp♀ (462-108), 1 p♀ (462-101) [UCLA].

25. *Aedes* (Howardina) *guerrero* Berlin, n.sp.

Figs. 6, 9, 49

TYPES: Holotype ♀ (MEX 166), 21 miles south of Chilpancingo, Guerrero, Mexico, 31 Aug 1964, E. Fisher [USNM]. Paratypes: 2 ♀ (MEX 166), same data as holotype [UCLA].

FEMALE. Wing: 3.06 mm. Proboscis: 2.34 mm. Forefemur: 2.16 mm. Abdomen: about 3.15 mm. In general similar to *allotecnnon*, differing apparently only in the following. *Head*: Erect scales on occiput whitish in middle, darker on sides. Palpus about 0.2 of proboscis, with white scales on apex and mesal side of segment 4. *Thorax* (fig. 9): Mesonotal light lines golden. Creamy scales on median scutellar lobes narrow distally, broader basally. Paratergite with broad silvery scales. Scales on *apn* broad, silvery; upper *ppn* with predominantly broad, silvery scales, creamy narrow ones restricted to upper border; lower *ppn* patch small, with broad silvery scales; *psp* usually with a small silvery patch; other scale patches bright silvery. *Legs*: Foretarsus and midtarsus with short incomplete white rings on segments 1, 2; hindtarsus with broader white rings on 1-3. *Haltere*: Stem pale, knob mostly creamy, with a few black basal scales. *Abdomen*: Basomedian tergal light scales white from segment III caudad, silvery on segments VI, VII. Sternites with broad basal V-shaped white scale patches, silvery on distal segments; apical white scales inconspicuous.

MALE. Unknown.

PUPA. Imperfectly known. Appears very similar to *allotecnnon* but possibly differentiated by the hair 5-IV, V which is shorter, barely extending beyond the apex of the following tergite.

LARVA (fig. 49). Head: 0.81 mm. Siphon: 0.7 mm. Anal Saddle: 0.3 mm. Readily separated from *allotecnnon* by the presence of abdominal spicules only on the ventral surface and anal saddle without distinct marginal spicules ventrad of hair 1-X. *Head*: Width subequal to length. Pigmentation as in *allotecnnon*. Mental plate with a strong median tooth and 13(12-14) distinct teeth on either side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(5, 5-6), 5(1, 1-2), 6(2), 7(2), 8(1), 9(2, 2-4), 10(2, 2-3), 11(7, 5-8), 12(2, 1-2), 13(1), 14(5, 4-8), 15(4, 3-4). *Antenna*: Length about 0.33 of head; shaft pigmentation moderate, spicules not apparent. All hairs except 1 single; 1-A (2) at about 0.6 from base. *Thorax*: Integument glabrous as in *allotecnnon*. Apices of long hairs attenuate; barbs present on both long and stellate hairs. Prothorax: hair 0(13, 11-15), 1(6, 3-7), 2(1), 3(13, 10-14), 4(2, 2-3), 5(1, 1-2), 6(2), 7(2), 8(21, 21-25), 9(17, 13-19), 10(1), 11(2, 2-4), 12(1), 13(15, 9-17), 14(34, 30-38). Mesothorax: hair 1(7, 4-7), 2(1), 3(1), 4(1), 5(1), 6(5, 5-6), 7(1), 8(7, 6-7), 9(8, 6-9), 10(1), 11(1), 12(1), 13(14, 10-16), 14(4, 3-7). Metathorax: hair 1(5, 4-6), 2(1), 3(5, 2-6), 4(9, 8-10), 5(9, 8-11), 6(1), 7(7, 6-8), 8(9, 6-11), 9(4), 10(1), 11(1), 12(1),

13(16, 11-17). *Abdomen*: Integument of segment I glabrous; other segments with spinelike spicules restricted to ventral surface; hairs 1,7,13-II-VII apparently not stellate. Segment I: hair 1(7, 4-8), 2(11, 10-15), 3(1), 4(4, 4-5), 5(12, 10-13), 6(3, 3-4), 7(1), 9(6, 5-9), 10(1), 11(11, 10-15), 13(5, 4-7). Segment II: hair 0(1), 1(4, 4-7), 2(9, 8-12), 3(1), 4(4, 4-6), 5(11, 9-12), 6(3, 3-4), 7(5, 4-7), 8(1), 9(5, 5-7), 10(1), 11(1), 12(1), 13(4, 4-5). Segment III: hair 0(1), 1(4, 3-5), 2(11, 8-11), 3(1), 4(1), 5(11, 9-12), 6(2), 7(5, 4-6), 8(1), 9(7, 5-9), 10(1), 11(1), 12(1), 13(4, 3-5), 14(1). Segment IV: hair 0(1), 1(4, 3-5), 2(10, 7-11), 3(1), 4(1), 5(10, 10-13), 6(2), 7(5, 5-7), 8(1), 9(8, 6-8), 10(1), 11(1), 12(1), 13(4, 4-5), 14(1). Segment V: hair 0(1), 1(4, 3-4), 2(8, 8-10), 3(1), 4(1, 1-2), 5(10, 8-11), 6(2), 7(5, 5-8), 8(1), 9(7, 5-9), 10(1), 11(1), 12(1), 13(5, 3-6), 14(1). Segment VI: hair 0(1), 1(3, 3-5), 2(8, 5-9), 3(1), 4(1), 5(9, 6-11), 6(2), 7(4, 3-5), 8(3, 3-4), 9(7, 6-9), 10(1), 11(1), 12(1), 13(5, 4-5), 14(1). Segment VII: hair 0(1), 1(3, 3-4), 2(8, 7-10), 3(1), 4(1), 5(7, 5-9), 6(3, 2-4), 7(1, 1-2), 8(5, 5-7), 9(5, 3-9), 10(1), 11(1), 12(1), 13(4, 3-5), 14(1). *Segment VIII*: Comb scales in a single row, usually 14(12-16) in number; individual scale elongate, pointed apically, evenly fringed almost to tip. Hair 0(1), 1(9, 4-11), 2(1), 3(7, 6-9), 4(1), 5(6, 5-7), 14(1). *Siphon*: Index about 3.3-3.6. Integument imbricate, moderately to strongly pigmented, with darker basal ring. Pecten extending to 0.42, usually with 18(17-22) teeth; individual tooth pointed apically, with basal denticles. Hair 1(3, 2-4), 2(1), 3-5 not visible, 6(1), 7(1), 8(2, 1-2), 9(1). *Anal Segment*: Saddle imbricate, moderately to strongly pigmented, with darker basal ring; caudal margin with spicules present only dorsad of hair 1-X. Gills subequal, long, more than 2.0 of saddle. Hair 1(4, 3-5), 2(5, 5-7), 3(2), 4a(4, 3-5), 4b(3, 3-4), 4c(3, 3-4), 4d(3, 2-3), 4e(2, 1-2).

SYSTEMATICS. Although closely resembling *allotecnnon*, this form appears to be a distinct species restricted to the Sierra Madre del Sur in Mexico where no other member of the group has been collected. The association of the immature stages with the females is presumptive only as no adults were obtained from the rearings and were found in a different locality from the adults but is probably correct since the larva is obviously of the *allotecnnon* type but with distinctive features as indicated in the diagnosis. The pupal stage is not described at this time as it is known only from 2 whole imperfect specimens from incomplete rearings. It also appears to be generally similar to *allotecnnon* but possibly differentiated by the shorter hair 5-IV-V.

BIONOMICS. The presumptive immature stages of *guerrero* have been collected in epiphytic bromeliads at elevations of about 7,200-7,800 feet (MEX 429,430,431, 434). The 3 females were taken in a biting-landing collection (MEX 166) at 0800 in a pine-oak woodland.

DISTRIBUTION (fig.6). Sierra Madre del Sur in Mexico at elevations above 7000 ft. Material examined: 20 specimens; 3 ♀, 2 pupae, 15 larvae; 2 incomplete individual rearings.

MEXICO. *Guerrero*: Chilpancingo, 21.0 mi S, 21 Aug 1964, E. Fisher, 3 ♀ (MEX 166, type series) [USNM, UCLA]. *Oaxaca*: Ixtlan de Juarez, El Punto, elev. 7700 ft, 13 Aug 1966, D.A. Schroeder (MEX 434), 1 IP (434-10); Vivero Rancho Teja, elev. 7200 ft, 12 Aug 1966, D.A. Schroeder, 1 IP (429-10), 7 L (MEX 429), 1 L (MEX 430), 5 L (MEX 431) [UCLA].

26. *Aedes* (*Howardina*) *guatemala* Berlin, n.sp.

Figs.6,9

TYPES: Holotype ♀ (GUA 138-13), Yepocapa, Chimaltenango, Guatemala, 20 July 1950, Mi-

guel Xinic and Pedro Garcia [USNM]. Paratypes: 4 ♀ (GUA 138-10,12,14,15), same data as holotype [UCLA].

FEMALE. Wing: 3.2 mm. Proboscis: 2.37 mm. Forefemur: 2.01 mm. Abdomen: about 2.6 mm. Very similar to *allotecnion*, differing apparently only in the following. *Head*: Erect scales on occiput predominantly dark, median ones lighter. *Thorax* (fig. 9): Mesonotal light lines pale golden. Lateral scutellar lobe with a few narrow dark and pale golden scales. Upper *ppn* scales predominantly creamy, narrow, a few scales slightly broader at lower border. *Legs*: Foretarsus and midtarsus with a few white scales on segment 1; hindtarsus with short white rings on segments 1 and 2 only. *Haltere*: Stem pale, knob predominantly white, dark scales restricted to base.

MALE, PUPA, and LARVA unknown.

SYSTEMATICS. The 6 known females of *guatemala* are so different in the details of ornamentation from other members of the *Allotecnion* Group that I do not hesitate in recognizing them as members of a distinct species even in the absence of immature stages. This species appears to be restricted to the Pacific slope of central Guatemala where no other species of *Howardina* has been recorded.

BIONOMICS. The immature stages will probably be found in epiphytic bromeliads. The females were probably taken in a biting-landing collection on human bait.

DISTRIBUTION (fig.6). Pacific slope of Guatemala. Material examined: 6 specimens; 6 ♀; no individual rearings or immature stages.

GUATEMALA. *Chimaltenango*: Yepocapa, 20 July 1950, Miguel Xinic and Pedro Garcia (GUA 138, type series), 5 ♀ (138-10,12,13-15); 24 July 1950, V.C. and R. Feoli, 1 ♀ (GUA 139) [USNM, UCLA].

Eleanorae Group

FEMALES. *Head*: Median light line on vertex usually with narrow scales (moderately broad in *eleanorae*). Proboscis distinctly longer than forefemur. Torus with a restricted mesal scale patch. *Thorax*: Mesonotal light lines usually creamy to golden (except in *ecuadoriensis* in which inner dorsocentral and lateral marginal lines are white); inner dorsocentral line complete; outer dorsocentral line usually shorter, not reaching anterior margin, subparallel to inner; lateral marginal line continuous; scales on anterior promontory creamy, golden or white. Antealar area above paratergite with golden scales. Paratergite with a moderate scale patch extending entire sclerite length. Upper *ppn* entirely covered with light scales; upper *stp* patch quadrate. *Legs*: Distal white spot on anterior surface of midfemur distinct; present or absent on hindfemur. Tibiae completely dark. *Wing*: Veins entirely dark scaled. *Abdomen*: Basomedian tergal light markings absent or present on III-VII.

MALES. Palpus with or without basomedian light scales on segments 4 and 5.

MALE GENITALIA. Lobe of tergite IX prominent or indistinct, with 4-7 strong bristles. Sidepieces separated at base by a distance less than width of aedeagus; without any indication of lobes on tergomesal or sternomesal margins. Claspette represented by a conical tubercle. Aedeagus shorter than or subequal to proctiger; apical emargination distinct or shallow, lateral lobes conspicuous or inconspicuous.

PUPAE. *Cephalothorax*: Trumpet moderate, index 4.5-6.4, not expanded apically; hairs 10,12-C varied in branching. *Abdomen*: Hair 5-IV-V moderate to long, sometimes exceeding apex of second tergite following; hair 9-VII moderate, reaching or exceeding lateral angle of tergite. *Paddle*: Moderate; apex usually rounded.

LARVAE. *Head*: Hairs 4-7-C varied in branching; 15-C moderate to long, always extending beyond base of mental plate. *Thorax*: Roundish in outline; spiculation dense, weak or absent, spicules hairlike, simple. *Abdomen*: Integument strongly or weakly uniformly spiculate. Hair 8-VII distinctly cephalodorsad of 9-VII. *Siphon*: Integument smooth or imbricate; acus distinct, separate. *Anal Segment*: Hair 3-X single or double; ventral brush with 5 pairs of hairs.

DISCUSSION. The Eleanorae Group of 6 species is probably derived from the Quadrivittatus Group and seems to replace the Allotecnion Group south of Panama. The ornamentation of the midfemur and hindfemur is quite varied in this group, more or less bridging the characteristic development in the other 2 groups. The larvae are also quite varied and somewhat intermediate between the Quadrivittatus and Allotecnion Groups, although the ventral brush always has only 5 pairs of hairs as in the latter group. Members of this group have been misidentified in the past as *quadrivittatus*.

The Eleanorae Group appears to be entirely confined to the Andes where it has been collected from moderate elevations up to nearly 11,000 feet. The group is now known from western and possibly northcentral Venezuela, Colombia, Ecuador and Bolivia (fig.6). Although seemingly some of the species are found sympatrically, there are indications of strong ecological divergence in other instances (*ecuadoriensis* and *brevivittatus* for example). This group is apparently sympatric to a limited extent with the Whitmorei Group in the north and with the Whitmorei and Aurivittatus Groups in the south.

27. *Aedes* (*Howardina*) *eleanorae* Berlin, n.sp.

Figs.6,9,50,51

TYPES: Holotype ♂ (COB 10-21) with associated pupal and larval skins and genitalia slide, Buritica, Antioquia, Colombia, 5000 ft, 8 Jan 1965, E. Osorno-Mesa [USNM]. Allotype ♀ (COB 10-20) with associated pupal and larval skins, same data as holotype [USNM]. Paratype ♀ (COB 10-22) with associated pupal and larval skins, same data as holotype [UCLA]. This species is dedicated to my wife, Eleanor, for her interests in and contribution to the study of this group.

Aedes (*Howardina*) *quadrivittatus* in part of Dyar (1928:229); Edwards (1932:155); Lane (1939:100; 1953:713); Reyes (1955:74,89); Stone, Knight and Starcke (1959:174).

FEMALE. Wing: 3.06 mm. Proboscis: 2.34 mm. Forefemur: 2.07 mm. Abdomen: 2.88 mm. *Head*: Scales on median stripe predominantly broad and white, a few anterior ones narrow; light scales on sides and venter white. Erect scales on occiput and sides creamy. Palpus about 0.16 of proboscis. Mesal light scale patch on torus creamy. *Thorax* (fig.9): All mesonotal light lines creamy, of uniform width throughout; outer dorsocentral line short, arising at anterior 0.25 and reaching scutellum; lateral marginal line long, from side of anterior promontory to wingbase, appearing broad from scutal angle to wingbase owing to presence of creamy scales in antealar area above paratergite; scales on anterior promontory creamy. Median scutellar lobe with broad dark scales laterally and broad creamy scales in the middle from base to apex; lateral lobes with a few narrow creamy scales. Scales on paratergite moderately broad, white. *Apn* scales broad, white, a few anterior ones narrower, creamy; upper *ppn* predominantly with narrow, curved scales, a few broader scales below; lower *ppn* patch distinct and merging with *ssp* patch; other scale patches pure white, distributed as in the

group. *Legs*: Forefemur dark anteriorly, predominantly dark posteriorly except for a creamy longitudinal line; midfemur with narrow anteromesal creamy line to 0.67 terminating in a white spot, posteriorly proximal 0.5 creamy, rest dark; hindfemur creamy to 0.67 on both sides, rest dark scaled. Foretarsus with a few white scales on segment 1; midtarsus with short incomplete white ring on 1; hindtarsus with broader white rings on 1 and 3, second segment dark. *Haltere*: Stem pale, knob predominantly white, a few dark scales dorsally. *Abdomen*: Basomedian tergal light scales absent. Sternites with broad V-shaped white patches; apical light scales inconspicuous.

MALE. Wing: 2.88 mm. Proboscis: 2.43 mm. Forefemur: 1.89 mm. Essentially similar to female in color. Palpus entirely dark.

MALE GENITALIA (fig.50). As figured; diagnostic characters as in the key. Ninth tergite lobe not prominent, with 4,5 strong bristles. Sidepiece length about 3.0 of median width. Clasper about 0.5 of sidepiece, with 1,2 subapical hairs; basal 0.3 with minute spicules; spiniform long, about 0.5 of clasper. Aedeagus shorter than proc-tiger; dorsal sclerotization emarginate apically, producing lateral sclerotized lobes.

PUPA (fig.50). Abdomen: 3.3 mm. Trumpet: 0.39 mm; index 4.4-4.5. Paddle: 0.67 mm. Readily separated from other members of the group (except *leei*) by the strongly developed hair 8-VII on dorsal surface; from *leei* by the branched hair 10-C. Chaetotaxy as given below, hairs moderately to darkly pigmented. *Cephalothorax*: Mesonotum lightly pigmented between trumpets, lateral areas and metanotum darker; trumpet moderately pigmented and sharply contrasting. Hair 1(1), 2(1), 3(1, 1-2), 4(3, 2-5), 5(2), 6(1, 1-2), 7(2), 8(1, 1-3), 9(1, 1-2), 10(6, 5-6), 11(1, 1-2), 12(4, 2-5). *Abdomen*: Tergite I moderately pigmented except for usual membranous areas; II-VII moderately pigmented, progressively lighter caudad. Segment I: hair 1(13-16 primary branches), 2(1, 1-3), 3(1), 4(2, 2-4), 5(1, 1-2), 6(1), 7(1, 1-2), 9(1, 1-3), 11(2, 2-3, present in some). Segment II: hair 0(1), 1(6, 4-7), 2(1), 3(1), 4(2, 2-3), 5(2, 1-2), 6(1), 7(2, 1-3), 9(1), 10 (present in a few). Segment III: hair 0(1), 1(2, 2-4), 2(2, 1-3), 3(1, 1-2), 4(1, 1-2), 5(1, 1-2), 6(1), 7(1, 1-2), 8(1, 1-3), 9(1), 10(1), 11(1), 14(1). Segment IV: hair 0(1), 1(2, 2-3), 2(1, 1-2), 3(3, 2-3), 4(1, 1-2), 5(2), 6(1), 7(1, 1-2), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment V: hair 0(1), 1(2), 2(1, 1-2), 3(2, 1-2), 4(2, 2-3), 5(2), 6(1), 7(2, 1-3), 8(2, 1-3), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(2, 1-2), 2(2, 1-2), 3(1, 1-2), 4(2, 1-2), 5(1), 6(1), 7(1, 1-2), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1, 1-2), 2(1, 1-2), 3(1, 1-2), 4(1), 5(1, 1-3), 6(3, 1-3), 7(1), 8(4, 3-5), 9(4, 4-8), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(11, 11-14), 14(1). *Paddle*: Lightly pigmented, midrib slightly darker; hair 1-P single. Male genital lobe extending to 0.5 of paddle, female genital lobe to 0.34.

LARVA (fig.51). Head: 0.63 mm. Siphon: 0.28 mm. Anal Saddle: 0.27 mm. Diagnostic characters as in the key. Readily separated from other members of the group by pecten teeth extending beyond hair 1-S. *Head*: Width subequal to length; pigmentation moderate except around mouthparts where it is deeper. Mental plate with a strong median tooth and usually 12 distinct teeth (11-12) on each side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(12, 9-15), 5(8, 6-9), 6(5, 4-6), 7(17, 14-18), 8(12, 10-14), 9(14, 13-16), 10(2, 2-3), 11(34, 20-42), 12(10, 7-10), 13(1), 14(18, 18-22), 15(2, 2-3). *Antenna*: Length about 0.5 of head; shaft uniformly lightly pigmented and with few scattered spicules; hair 1(3, 2-3), others single. *Thorax*: Integument densely covered with hairlike simple or branched spicules except on intersegmental areas; long hairs barbed and with attenuate apices; stellate hairs with many weakly barbed branches. Prothorax: hair 0(30, 27-34), 1(5, 3-5), 2(1), 3(42, 35-42), 4(2, 1-2), 5(1), 6(1), 7(2), 8(30, 28-34), 9(22, 18-24), 10(1), 11(2, 2-

3), 12(1), 13(36, 31-36), 14(52, 48-62). Mesothorax: hair 1(27, 23-32), 2(1), 3(1), 4(1), 5(1), 6(4, 3-5), 7(1), 8(4, 4-6), 9(5, 5-7), 10(1), 11(1, 1-2), 12(1), 13(22, 18-23), 14(22, 18-26). Metathorax: hair 1(37, 34-40), 2(1), 3(23, 20-26), 4(22, 15-25), 5(21, 17-23), 6(1), 7(4, 4-5), 8(23, 23-35), 9(3, 3-4), 10(1), 11(1, 1-3), 12(1), 13(26, 24-30). *Abdomen*: Integument and stellate hairs as on thorax. Segment I: hair 1(28, 25-28), 2(28, 26-30), 3(1), 4(1), 5(24, 22-25), 6(3, 2-3), 7(1), 9(12, 10-15), 10(1), 11(24, 20-24), 13(30, 29-35). Segment II: hair 0(1), 1(30, 29-31), 2(30, 24-32), 3(1), 4(1), 5(29, 25-30), 6(3), 7(20, 19-29), 8(1), 9(17, 16-17), 10(1), 11(1), 12(1), 13(36, 30-40). Segment III: hair 0(1), 1(30, 28-32), 2(31, 26-34), 3(1), 4(1), 5(28, 25-30), 6(2), 7(22, 17-23), 8(1), 9(22, 21-25), 10(1), 11(1), 12(1), 13(30, 30-33), 14(1). Segment IV: hair 0(1), 1(32, 27-32), 2(29, 26-35), 3(1), 4(1), 5(30, 24-32), 6(2), 7(22, 18-22), 8(1), 9(26, 22-27), 10(1), 11(1), 12(1), 13(28, 26-29), 14(1). Segment V: hair 0(1), 1(28, 28-31), 2(30, 28-33), 3(1), 4(1), 5(30, 23-31), 6(2), 7(22, 16-25), 8(1), 9(26, 25-26), 10(1), 11(1), 12(1), 13(30, 29-33), 14(1). Segment VI: hair 0(1), 1(30, 30-32), 2(28, 28-33), 3(1), 4(1), 5(30, 27-30), 6(1), 7(20, 12-21), 8(1), 9(26, 22-26), 10(1), 11(1), 12(1), 13(26, 23-38), 14(1). Segment VII: hair 0(1), 1(30, 28-33), 2(30, 24-30), 3(1), 4(1), 5(29, 24-29), 6(14), 7(1), 8(24, 20-25), 9(24, 18-24), 10(1, 1-2), 11(1), 12(1), 13(28, 24-28), 14(1). *Segment VIII*: Comb scales in a single row, usually 12(12-14) in number; individual scale long, pointed apically and fringed almost to tip. Hair 0(1), 1(33, 28-34), 2(1), 3(9, 8-9), 4(1), 5(32, 27-35), 14(1). *Siphon*: Index about 3.3; integument imbricate, moderately pigmented except for darker basal ring. Pecten teeth usually 21(19-23), extending beyond hair 1-S to about 0.7 of siphon; individual tooth with basal denticles. Hair 1(4, 3-5), 2(1), 3-5 not visible, 6(1), 7(1), 8(1, 1-2), 9(1). *Anal Segment*: Saddle moderately uniformly pigmented except for darker basal ring; integument with minute spicules; caudal margin with spines of varying length. Gills subequal, moderately long, about 2.0 of saddle length, narrow. Hair 1(2, 2-3), 2(4, 3-4), 3(1), 4a(2), 4b(2), 4c(2), 4d(2), 4e(1).

SYSTEMATICS. *A. eleanorae* is the most strongly differentiated member of the group as indicated in the diagnosis above and in the keys. At present it is known from only 2 localities in Colombia, Buritica in the northern part of the Cordillera Occidental, and Buena Vista in the upper part of the Orinoco basin on the eastern slope of the Cordillera Oriental. Although *eleanorae* may be broadly sympatric with *osornoi* and *marinkellei*, it has not been found associated with these species and apparently occurs at lower elevations.

BIONOMICS. The breeding sites of *eleanorae* are in epiphytic bromeliads at elevations of about 5,000 feet (COB 10). The female from Buena Vista was probably taken in a biting-landing daytime collection.

DISTRIBUTION (fig.6). Upper Magdalena and Orinoco drainages in Colombia. Material examined: 15 specimens; 1 ♂, 3 ♀, 4 pupae, 7 larvae; 3 individual larval rearings).

COLOMBIA. *Antioquia*: Buritica, elev. 5000 ft, 8 Jan 1965, E. Osorno-Mesa (COB 10, type series), 1 lp♂ (10-21), 2 lp♀ (10-20,22); 15 Jan 1965, E. Osorno-Mesa, 1 p, 1 L, 3 l [USNM, UCLA]. *Meta*: Villavicencio, Buena Vista, 4 June 1942, W.H.W. Komp, 1 ♀ [UCLA].

28. *Aedes* (Howardina) *marinkellei* Berlin, n.sp.

Figs.6,9,52,53

TYPES: Holotype ♀ with associated pupal and larval skins (COM 63-19), Suba, Bogota, Cundinamarca, Colombia, 8300 ft, 16 Apr 1966, C.J. Marinkelle [USNM]. Paratypes: 1 ♀ (63-15) with

associated pupal and larval skins, 7 larvae, same data as holotype [UCLA]. This species is dedicated to Dr. C.J. Marinkelle for his contributions to the study of neotropical mosquitoes.

Aedes (Howardina) quadrivittatus in part of Dyar (1928:229); Edwards (1932:155); Lane (1939:100; 1953:713); Reyes (1955:74,89); Stone, Knight and Starcke (1959:174).

FEMALE. Wing: 3.85 mm. Proboscis: 3.06 mm. Forefemur: 2.19 mm. Abdomen: about 3.41 mm. Similar to *eleanorae*, differing chiefly in the following. *Head*: Light scales on median stripe and short orbital line narrow, creamy; light scales on sides and venter broad, creamy. Erect scales predominantly creamy, darker on sides. Palpus about 0.16 of proboscis; predominantly dark, apex and mesal surface of segment 4 white scaled. Mesal patch on torus creamy. *Thorax* (fig.9): All mesonotal light lines creamy; outer dorsocentral line complete, broader on anterior 0.5, merging with lateral marginal line at level of lateral prescutal area; lateral marginal line long, moderately broad, extending from area of humeral bristle to wingbase; scales on anterior promontory creamy. Light scales on median scutellar lobe broad, white from base to apex; lateral lobes with a few narrow dark scales. Scales on paratergite moderately broad, creamy. *Apn* scales predominantly broad, dingy white, a few anterior ones narrower; *ppn* with only an upper patch of predominantly narrow creamy scales, a few lower ones whitish, broader; upper *stp* patch larger than in *eleanorae*; other scale patches white, distributed as in *eleanorae*. *Legs*: Forefemur predominantly dark anteriorly except for a few scattered whitish scales along whole length, posterior surface mostly creamy except for a narrow dark line from base to apex; midfemur predominantly dark anteriorly except for a few basal creamy scales and a white spot at distal 0.67, posteriorly mostly creamy with scattered dark scales on distal 0.5; hindfemur creamy to 0.67 on both sides, rest dark scaled. Foretarsus and midtarsus with basal white scales on segments 1,2; hindtarsus with broader white rings on segments 1-3. *Haltere*: Stem whitish, knob predominantly white, a few basal scales dark. *Abdomen*: Basomedian tergal light scales dingy white. Sternites with large basal patches of dingy white scales; median apical white scales distinct to VI, on segment VII few and indistinct. Cercus with a few apical white scales.

MALE unknown.

PUPA (fig.52). Abdomen: 4.6 mm. Trumpet: 0.51 mm; index about 4.5. Paddle: 0.86 mm. Chaetotaxy as given below, hairs moderately to darkly pigmented. Distinguished from *osornoi* by metanotal hairs all single, from *leei* and *eleanorae* by ventrally placed hair 8-VII. *Cephalothorax*: Mesonotum moderately pigmented between trumpets, lateral areas and metanotum darker; trumpets strongly contrasting. Hair 1(1), 2(1), 3(1), 4(3), 5(2), 6(1), 7(2, 2-3), 8(1), 9(1), 10(1), 11(1), 12(1). *Abdomen*: Tergite I moderately pigmented except for usual membranous areas; rest of segments moderate, pigmentation progressively lighter caudad. Segment I: hair 1(6-7 primary branches, each with many secondary ones), 2(1), 3(1), 4(2, 1-2), 5(2), 6(1), 7(1), 9(1), 11(1). Segment II: hair 0(1), 1(2, 1-2), 2(1), 3(1), 4(1), 5(1), 6(1), 7(1), 9(1). Segment III: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1, 1-2), 5(1), 6(1), 7(1, 1-2), 8(1), 9(1), 10(1), 11(1), 14(1). Segment IV: hair 0(1), 1(1, 1-2), 2(1), 3(2), 4(2, 1-2), 5(2), 6(1), 7(1, 1-2), 8(1), 9(1), 10(1), 11(1), 14(1). Segment V: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1), 5(1), 6(1), 7(2), 8(1), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1), 6(1), 7(1), 8(1), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1), 6(1), 7(1), 8(1), 9(2), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(5, 5-7), 14(1). *Paddle*: Uniformly lightly pigmented, midrib darker; external margin serrated; apex rounded; hair 1-P slender. Female genital lobe extending to 0.31 of paddle.

LARVA (fig.53). Head: 0.93 mm. Siphon: 0.81 mm. Anal Saddle: 0.32 mm. Chaetotaxy as given below, hairs moderately to darkly pigmented. Readily separated from all other members of *Eleanorae* Group by hair 5-C always double. *Head*: Width subequal to length; pigmentation moderate except around mouthparts where it is deeper. Mental plate with a strong median tooth and 10,11 distinct teeth on either side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(6, 5-6), 5(2), 6(3, 3-4), 7(5, 4-6), 8(1), 9(2, 2-4), 10(2), 11(12, 8-12; stellate, branches of varied lengths), 12(1), 13(1), 14(6, 4-8), 15(2). *Antenna*: Length about 0.33 of head; pigmentation moderate; shaft with scattered spicules. All hairs except 1 single; hair 1-A (2, 2-3) at about 0.58 from base. *Thorax*: Integument sparsely covered with simple, hairlike spicules. Apices of long hairs attenuate; long and stellate hairs weakly barbed. Prothorax: hair 0(17, 13-22), 1(3), 2(1), 3(20, 19-22), 4(2, 1-2), 5(1), 6(1), 7(2), 8(15, 10-16), 9(11, 9-13), 10(1), 11(1, 1-3), 12(1), 13(17, 16-20), 14(34, 34-38). Mesothorax: hair 1(7, 6-8), 2(1), 3(1), 4(1), 5(1), 6(4, 3-5), 7(1), 8(6, 5-6), 9(6, 4-8), 10(1), 11(1), 12(1), 13(10, 8-11), 14(2, 1-3). Metathorax: hair 1(9, 6-9), 2(1), 3(3, 2-4), 4(9, 8-10), 5(10, 7-10), 6(1), 7(6, 5-7), 8(9, 8-10), 9(3), 10(1), 11(1), 12(1), 13(12, 10-18). *Abdomen*: Integument and stellate hairs as in thorax. Segment I: hair 1(13, 11-19), 2(8, 8-11), 3(1), 4(1), 5(10, 9-16), 6(3, 2-3), 7(1), 9(2, 2-3), 10(1), 11(13, 11-14), 13(6, 4-8). Segment II: hair 0(1), 1(16, 12-16), 2(9, 8-11), 3(1), 4(1), 5(10, 8-12), 6(3), 7(6, 5-6), 8(1), 9(6, 5-7), 10(1), 11(1), 12(1), 13(9, 8-10). Segment III: hair 0(1), 1(15, 11-16), 2(10, 10-12), 3(1), 4(1), 5(13, 11-14), 6(2), 7(8, 7-10), 8(1), 9(11, 6-11), 10(1), 11(1), 12(1), 13(11, 8-12), 14(1). Segment IV: hair 0(1), 1(15, 13-17), 2(12, 9-13), 3(1), 4(1), 5(12, 10-13), 6(2), 7(9, 7-10), 8(1), 9(11, 9-13), 10(1), 11(1), 12(1), 13(11, 8-12), 14(1). Segment V: hair 0(1), 1(14, 12-16), 2(10, 10-13), 3(1), 4(1), 5(12, 9-13), 6(2), 7(9, 6-9), 8(1), 9(11, 11-15), 10(1), 11(1), 12(1), 13(10, 9-11), 14(1). Segment VI: hair 0(1), 1(14, 11-16), 2(10, 9-12), 3(1), 4(1), 5(11, 10-13), 6(2), 7(5, 5-8), 8(1), 9(12, 10-14), 10(1), 11(1), 12(1), 13(9, 7-9), 14(1). Segment VII: hair 0(1), 1(10, 9-15), 2(10, 10-13), 3(1), 4(1), 5(10, 8-11), 6(5, 4-6), 7(1), 8(5, 5-6), 9(8, 5-10), 10(1), 11(1), 12(1), 13(5, 4-6), 14(1). *Segment VIII*: Comb scales in a single row, usually 14(14-18) in number; individual scale long, pointed apically, fringed nearly to tip. Hair 0(1), 1(7, 7-11), 2(1), 3(5, 3-6), 4(1), 5(6, 6-9), 14(1). *Siphon*: Index about 3.0-3.2; moderately pigmented, imbricate. Pecten extending to about 0.5, usually with 16(16-19) teeth; individual tooth with basal denticles. Hair 1(1, 1-2), 2(1), 3-5 not visible, 6(1), 7(1), 8(1), 9(1). *Anal Segment*: Saddle moderately pigmented, with darker basal ring; caudal margin with spines of varying sizes. Gills subequal, at least 3.0 of saddle length, fingerlike. Hair 1(1), 2(4, 3-4), 3(2, 2-3), 4a(2, 2-3), 4b(2), 4c(2, 1-2), 4d(2, 1-2), 4e(2).

SYSTEMATICS. *A. marinkellei* is most similar to *osornoi* and *leei* but is readily separated from both by constant diagnostic features in all known stages. It is known at present only from Cundinamarca Province in Colombia at elevations of over 8,000 feet where it is sympatric with *osornoi*. As indicated under the latter, a single reared female from this area combines features of *osornoi* in adult ornamentation and of *marinkellei* in the immature stages, suggesting hybridization between the 2 forms. Although found in the same general locality, *osornoi* and *marinkellei* have not been collected together in the same bromeliad axils. It appears, therefore, that some ecological barrier usually separates the 2 species.

BIONOMICS. Immature stages of *marinkellei* have been found in the axils of epiphytic bromeliads at elevations above 8,000 feet. Judging by the adult collection, females of this species are apparently at least occasionally attracted to humans.

DISTRIBUTION (fig.6). Cordillera Oriental in Colombia. Material examined: 22

specimens; 11 ♀, 2 pupae, 9 larvae; 2 larval individual rearings.

COLOMBIA. *Cundinamarca*: Bogota, 1918, Fr. Apollinaire-Marie, 1 ♀; B.G. Amortegui, 1 ♀ [USNM]. Rio San Francisco, 21 May 1942, W.H.W. Komp, 7 ♀ [USNM, UCLA]. Suba, elev. 8300 ft, 16 Apr 1966, C.J. Marinkelle (COM 63, type series), 2 lp♀ (63-15,19), 7 L [USNM, UCLA].

29. *Aedes* (*Howardina*) *leei* Berlin, n.sp.

Figs. 6, 9, 54, 55

TYPES: Holotype ♀ (COL 17), 17.5 miles S.E. of Purace, Huila, Colombia, 10,000 ft, 28 Oct 1964, V.H. Lee [USNM]. Paratypes: 32 ♀ (COL 17), same data as holotype [USNM, BM, UCLA]. This species is dedicated to Dr. V.H. Lee, in recognition of his contributions to the study of neotropical mosquitoes.

Aedes (*Howardina*) *quadrivittatus* of Martinez and Prosen (1953:28,30; 1955:33-35; 1959:603, 605); Martinez, Carcavallo and Prosen (1960:25); Reyes (1955:74,89); Prosen, Carcavallo and Martinez (1964:105).

FEMALE. Wing: 5.04 mm. Proboscis: 3.15 mm. Forefemur: 2.88 mm. Abdomen: about 4.32 mm. Similar to *eleanorae* but larger and differing primarily in the following. *Head*: Light scales on median stripe and short orbital line narrow, pale golden; light scales on sides and venter creamy. Erect scales dull creamy. Palpus about 0.17 of proboscis; predominantly dark, apex and mesal surface of segment 4 creamy. Mesal patch on torus creamy. *Thorax* (fig.9): All mesonotal light lines golden; outer dorsocentral line incomplete, extending from anterior 0.25 to scutellum; lateral marginal line long, extending from side of anterior promontory to wingbase; scales on anterior promontory golden. Light scales on median scutellar lobe narrow, golden; lateral lobes with a few narrow dark scales. Scales on paratergite broad, creamy. *Apn* scales predominantly broad, creamy, a few anterior ones narrower, pale golden; *ppn* with only an upper patch of predominantly narrow golden scales; a few lower ones broader; other patches dingy white, distributed as in *eleanorae*. *Legs*: Forefemur dark anteriorly except for basal creamy scales, posterior surface with a creamy line broad to 0.5, narrowed distally, rest dark; midfemur mostly dark anteriorly except for basal creamy scales and a dingy white spot at distal 0.67, posteriorly proximal 0.6 creamy, rest dark; hindfemur creamy to 0.67 on both sides, rest dark scaled. Foretarsus with a few white scales on segment 1; midtarsus with short incomplete white rings on 1,2; hindtarsus with broader white rings on segments 1-3. *Haltere*: Stem pale, knob mostly dark, fringe scales whitish. *Abdomen*: Basomedian tergal light scales distinct; dingy white on segments II-VI, white on VII. Sternites with basal creamy patch; VI, VII with subapical band of white scales; apical light scales inconspicuous.

MALE. Wing: 5.04 mm. Proboscis: 3.69 mm. Forefemur: 2.7 mm. Essentially similar to female in color. Palpus predominantly dark, with basoventral white scales on segments 4 and 5.

MALE GENITALIA (fig.54). As figured; diagnostic characters as in the key. Ninth tergite lobe prominent, with 5,6 strong setae. Sidepiece length about 3.0 of median width. Clasper about 0.62 of sidepiece, with 2,3 subapical hairs; spiniform short, about 0.25 of clasper. Aedeagus subquadrate, longer than proctiger; dorsal sclerotization emarginate, producing lateral apical sclerotized lobes.

PUPA (fig.54). Abdomen: 4.12 mm. Trumpet: 0.63 mm; index about 5.3. Paddle: 0.99 mm. Diagnostic characters as in the key. Chaetotaxy as given below, hairs moderately to darkly pigmented. Readily distinguished from *eleanorae* and *osornoi* by all

metanotal hairs single; from *marinkellei* by dorsally placed hair 8-VII. *Cephalothorax*: Mesonotum moderately pigmented between trumpets, lateral areas and metanotum darker; trumpets strongly contrasting. Hair 1(1), 2(1), 3(1), 4(2, 2-3), 5(2), 6(1), 7(1, 1-2), 8(1), 9(1), 10(1), 11(1), 12(1). *Abdomen*: Tergite I strongly pigmented except for usual membranous areas; rest of segments with moderate to strong pigmentation, progressively lighter caudad. Segment I: hair 1(9-12 primary branches, each with many secondary ones), 2(1), 3(1), 4(1, 1-2), 5(1, 1-2), 6(1), 7(1), 9(1). Segment II: hair 0(1), 1(2, 1-3), 3(1, 1-2), 4(2), 5(1), 6(1), 7(1), 8(1), 9(1). Segment III: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(2), 6(1), 7(1, 1-2), 8(1), 9(1), 10(1), 11(1), 14(1). Segment IV: hair 0(1), 1(1, 1-3), 2(1), 3(1, 1-2), 4(1), 5(2), 6(1), 7(1, 1-2), 8(1), 9(1), 10(1), 11(1), 14(1). Segment V: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(2), 6(1), 7(2), 8(1), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(2), 3(1), 4(1), 5(1), 6(1), 7(1), 8(1), 9(1, 1-2), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1, 1-2), 2(1), 3(1), 4(1), 5(1), 6(2, 1-2), 7(1), 8(1), 9(4, 2-4), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1), 9(7, 6-7), 14(1). *Paddle*: Uniformly moderately pigmented, midrib darker; external margin serrated; apex faintly emarginate; hair 1-P slender. Male genital lobe extending to 0.44 of paddle, female genital lobe to 0.31.

LARVA (fig.55). Head: 0.94 mm. Siphon: 1.05 mm. Anal Saddle: 0.28 mm. Diagnostic characters as in the key. Chaetotaxy as given below; hairs moderately to darkly pigmented. Readily separated from *marinkellei* by hair 5-C single; from *osornoi* by hair 3-X double; from *eleanorae* by pecten teeth terminating before hair 1-S. *Head*: Width subequal to length; pigmentation strong except around mouthparts where it is deeper. Mental plate with a strong median tooth and usually 12(12-14) distinct teeth on either side, often a smaller detached tooth at base. Hair 0(1), 1(1), 3(1), 4(7, 4-7), 5(1, 1-2), 6(3, 2-3), 7(4, 4-5), 8(1, 1-2), 9(3), 10(3, 2-3), 11(16, 10-16, stellate, branches of varying length), 12(1), 13(1), 14(15, 10-19), 15(1, 1-2). *Antenna*: Length about 0.38 of head; pigmentation strong; shaft with a few scattered spicules. All hairs except 1, single; hair 1-A (2, 2-3) at about 0.64 from base. *Thorax*: Integument weakly spiculate, spicules hairlike. Apices of long hairs attenuate; barbs present on long and stellate hairs. Prothorax: hair 0(26, 26-44), 1(2, 1-2), 2(1), 3(44, 34-72), 4(1, 1-2), 5(1), 6(1), 7(2), 8(24, 23-36), 9(24, 13-34), 10(1), 11(1, 1-3), 12(1), 13(34, 29-51), 14(36, 36-50). Mesothorax: hair 1(20, 9-32), 2(1), 3(1), 4(1), 5(1), 6(5, 4-6), 7(1), 8(6, 3-8), 9(7, 6-8), 10(1), 11(1), 12(1), 13(18, 15-29), 14(13, 3-21). Metathorax: hair 1(26, 21-44), 2(1), 3(4, 3-5), 4(18, 16-30), 5(16, 14-20), 6(1), 7(5, 3-7), 8(16, 14-20), 9(3), 10(1), 11(1, 1-2), 12(1), 13(26, 20-46). *Abdomen*: Integument and stellate hairs as on thorax. Segment I: hair 1(22, 21-40), 2(27, 17-37), 3(1), 4(1), 5(14, 10-26), 6(2, 2-3), 7(1), 9(1, 1-2), 10(1), 11(20, 17-36), 13(19, 14-24). Segment II: hair 0(1), 1(22, 19-45), 2(23, 17-46), 3(1), 4(1), 5(16, 11-26), 6(3, 2-3), 7(11, 9-17), 8(1), 9(9, 8-20), 10(1), 11(1), 12(1), 13(18, 16-23). Segment III: hair 0(1), 1(22, 22-50), 2(22, 18-47), 3(1), 4(1), 5(15, 14-32), 6(1, 1-2), 7(11, 8-20), 8(1), 9(20, 16-34), 10(1), 11(1), 12(1), 13(25, 16-36), 14(1). Segment IV: hair 0(1), 1(24, 21-49), 2(22, 20-47), 3(1), 4(1), 5(16, 13-31), 6(1, 1-2), 7(10, 9-18), 8(1), 9(22, 18-33), 10(1), 11(1), 12(1), 13(25, 18-40), 14(1). Segment V: hair 0(1), 1(20, 18-46), 2(22, 18-45), 3(1), 4(1), 5(18, 14-26), 6(1), 7(10, 8-19), 8(1), 9(18, 16-31), 10(1), 11(1), 12(1), 13(24, 17-41), 14(1). Segment VI: hair 0(1), 1(24, 22-40), 2(22, 20-40), 3(1), 4(1), 5(16, 11-24), 6(1), 7(8, 8-16), 8(1), 9(20, 18-31), 10(1), 11(1), 12(1), 13(16, 12-16), 14(1). Segment VII: hair 0(1), 1(24, 18-27), 2(18, 16-27), 3(1), 4(1), 5(16, 12-19), 6(8, 8-11), 7(1), 8(10, 10-14), 9(17, 15-21), 10(1), 11(1), 12(1), 13(15, 13-15), 14(1). *Segment VIII*: Comb scales in a single row, usually 14(12-15) in number; individual scale long, pointed apically, fringed nearly to tip. Hair 0(1), 1(24, 19-24),

2(1), 3(7, 6-8), 4(1), 5(19, 11-21), 14(1). *Siphon*: Index about 3.8-4.3; integument imbricate, strongly pigmented, with darker basal ring. Pecten extending to about 0.5, usually 23(22-24) teeth; individual tooth with basal denticles. Hair 1(3, 2-3), 2(1), 3-5 not visible, 6(1), 7(1), 8(1), 9(1). *Anal Segment*: Saddle strongly pigmented, with darker basal ring; caudal margin with spines of varying sizes. Gills subequal, fingerlike, about 2.0 of saddle length. Hair 1(3, 2-4), 2(4, 3-5), 3(2), 4a(2), 4b(2), 4c(2), 4d(2), 4e(2, 1-2).

SYSTEMATICS. *A. leei* appears to be closely related to *osornoi* and *marinkellei*. It is sharply differentiated ecologically from the other 2 species, occurring apparently at considerably higher elevations in the paramo. All the stages are known from the type locality of Paramo de Purace in southern Colombia at elevations of 9600-10,500 ft (COL 16,17,19,52,53,54). The only other definite record is a single female from Zongo near La Paz, Bolivia. It seems very probable that this species will eventually be found in the intermediate area in Ecuador and Peru.

BIONOMICS. The immature stages have been collected in epiphytic and terrestrial bromeliads in the Paramo de Purace where a number of females were also taken biting-landing and entering a car between 1715 and 1815 hrs.

DISTRIBUTION (fig.6). Paramo in southern Colombia and Bolivia, above 9000 ft. Material examined: 188 specimens; 1 ♂, 34 ♀, 31 pupae, 122 larvae; 6 individual rearings (2 pupal, 4 incomplete).

BOLIVIA. *Cochabamba*: Chapare, Yungas del Palmar, elev. 3200 m, 1 ♀ (Prosen, Carcavallo and Martinez 1964:104). *La Paz*: Zongo, 1 Apr 1946, W.H.W. Komp, 1 ♀ [USNM].

COLOMBIA. *Cauca*: Paramo de Purace, 9600-10,500 ft, 18 Feb 1965, V.H. Lee (COL 52), 1 p♀ (52-101), 4 IP (52-18,19,29,36), 8 P, 38 L; 19 Feb 1965, V.H. Lee, 7 L (COL 53), 5 P, 36 L (COL 54) [UCLA]. *Huila*: 10.0-17.5 mi S.E. of Purace, 9600-10,500 ft, 28 Oct 1964, V.H. Lee, 1 p♂ (16-100), 33 ♀ (COL 17, type series); 30 Oct 1964, V.H. Lee, 9 P, 25 L, 1 I (COL 19), 3 P, 11 L (COL 20) [USNM, BM, UCLA].

30. *Aedes* (*Howardina*) *osornoi* Berlin, n.sp.

Figs.6,9,56,57

TYPES: Holotype ♂ (COB 37-16) with associated pupal and larval skins and genitalia slide, "Chorro de Padilla," Rio San Francisco, Bogota, Cundinamarca, Colombia, elev. 8200 ft, 14 July 1965, J.A. Ochoa [USNM]. Allotype ♀ (COB 37-10) with associated pupal and larval skins, same data as holotype [USNM]. Paratypes: 2 ♂ (COB 37-11,12), 2 ♀ (37-17,18), with associated pupal and larval skins, same data as holotype [BM, UCLA]. This species is dedicated to Dr. E. Osorno-Mesa, in recognition of his important contributions to the knowledge of neotropical mosquitoes.

Aedes (*Howardina*) *quadrivittatus* in part of Dyar (1928:229); Edwards (1932:155); Lane (1939:100; 1953:713); Reyes (1955:74,89); Stone, Knight and Starcke (1959:174); Cova Garcia, Sutil and Rausseo (1966a:58,283; 1966b:12,141,171,334).

FEMALE. Wing: 3.8 mm. Proboscis: 3.24 mm. Forefemur: 2.34 mm. Abdomen: about 3.8 mm. Similar to *eleonorae* but generally larger and differing mainly in the following. *Head*: Light scales on median stripe and short orbital line narrow, pale golden; light scales on sides and venter creamy. Erect scales predominantly pale golden, a few on sides darker. Palpus about 0.15 of proboscis; predominantly dark, with white scales on apex and mesal surface of segment 4. Mesal scale patch on torus creamy. *Thorax* (fig.9): All mesonotal light lines golden; outer dorsocentral line joined anteriorly to entire lateral prescutal area in fossa, gradually narrowed caudad

to scutellum; lateral marginal line separate only from scutal angle to wingbase; scales on anterior promontory golden. Light scales on median scutellar lobe predominantly narrow, pale golden, a few basal ones broader; lateral lobe with a few narrow dark and creamy scales. Scales on paratergite golden, moderately broad. *Apn* scales predominantly broad, pale golden, but a few anterior scales narrower; *ppn* only with an upper patch of narrow golden scales; *psp* scales narrow, pale golden; other patches pure white and distributed as in *eleanorae*. *Legs*: Forefemur predominantly dark anteriorly except for a few basal creamy scales, posterior surface mostly dark except for creamy longitudinal line from base to apex; midfemur dark anteriorly except for a few basal creamy scales and a dingy white spot at about 0.5, posterior surface creamy in basal 0.5 and along a narrow distal line, rest dark; hindfemur creamy in basal half. Foretarsus with white scales on segments 1,2; midtarsus with short incomplete white rings on 1,2, occasionally a few white scales on 3; hindtarsus with broader white rings on 1-3. *Haltere*: Stem pale, knob predominantly creamy, a few dorsal scales dark. *Abdomen*: Basomedian tergal light scales absent. Sternites with broad basal V-shaped silvery white patches; apical white scales inconspicuous.

MALE. Wing: 4.5 mm. Proboscis: 3.24 mm. Forefemur: 2.16 mm. Essentially similar to female in color. Palpus entirely dark.

MALE GENITALIA (fig.56). As figured; diagnostic characters as in the key. Ninth tergite lobe prominent, with 5-7 strong setae. Sidepiece length 2.5-3.0 of median width. Clasper about 0.67 of sidepiece, with 2 subapical hairs; spiniform moderate, length about 0.33 of clasper. Aedeagus subquadrate, shorter than proctiger; dorsal sclerotization shallowly emarginate, lateral lobes inconspicuous.

PUPA (fig.56). Abdomen: 4.29 mm. Trumpet: 0.61 mm; index 6.3-6.4. Paddle: 0.94 mm. Chaetotaxy as given below, hairs moderately to darkly pigmented. Distinguishable from *leei* and *marinkellei* by hairs 10,12-C branched; from *eleanorae* by the ventrally placed hair 8-VII. *Cephalothorax*: Mesonotum lightly pigmented between trumpets; lateral areas and metanotum slightly darker; trumpets strongly contrasting. Hair 1(1), 2(1), 3(1), 4(3, 1-4), 5(2, 1-3), 6(1, 1-2), 7(2, 1-3), 8(2, 1-3), 9(1), 10(3, 1-4), 11(1), 12(2, 1-4). *Abdomen*: Tergite I moderately pigmented except for usual membranous areas; tergites II,III also moderately pigmented, distal segments progressively lighter caudad. Segment I: hair 1(12-21 primary branches, subequal in length and each with a few branches), 2(1, 1-3), 3(1), 4(2, 2-3), 5(2, 1-3), 6(1), 7(1), 9(1), 11(1, 1-2 only occasionally present). Segment II: hair 0(1), 1(9, 3-19), 2(1, 1-2), 3(1), 4(2, 1-3), 5(1, 1-2), 6(1), 7(1, 1-2), 8(1, 1-2), 9(1). Segment III: hair 0(1), 1(3, 2-5), 2(1, 1-3), 3(1, 1-2), 4(1, 1-2), 5(1, 1-2), 6(1), 7(2, 1-2), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment IV: hair 0(1), 1(2, 1-2), 2(1, 1-2), 3(3, 2-3), 4(1), 5(2, 2-3), 6(1), 7(2, 1-2), 8(1, 1-2), 9(1), 10(1), 11(1), 14(1). Segment V: hair 0(1), 1(1), 2(1, 1-3), 3(1), 4(2, 1-2), 5(2, 1-2), 6(1), 7(2, 1-3), 8(2, 1-2), 9(1), 10(1), 11(1), 14(1). Segment VI: hair 0(1), 1(1), 2(1, 1-2), 3(1), 4(1, 1-2), 5(1, 1-2), 6(1), 7(1, 1-2), 8(2, 1-3), 9(1), 10(1), 11(1), 14(1). Segment VII: hair 0(1), 1(1), 2(1), 3(1), 4(1), 5(1), 6(2, 1-2), 7(1), 8(2, 1-3), 9(3, 2-4), 10(1), 11(1), 14(1). Segment VIII: hair 0(1), 4(1, 1-3), 9(8, 5-9), 14(1, 1-2). *Paddle*: Uniformly lightly pigmented, midrib darker; external margin serrated and apex rounded; hair 1-P slender. Male genital lobe extending to about 0.47 of paddle, female genital lobe to 0.3.

LARVA (fig.57). Head: 0.99 mm. Siphon: 0.91 mm. Anal Saddle: 0.33 mm. Readily separated from other members of the group by hair 3-X single. Chaetotaxy as given below. *Head*: Width subequal to length; pigmentation moderate except around mouthparts where it is deeper. Mental plate with a strong median tooth and 11 distinct teeth on either side, often a smaller detached tooth at base. Hair 0(1), 1(1),

3(1), 4(6, 4-8), 5(1), 6(3, 3-4), 7(4, 4-5), 8(1), 9(2, 1-2), 10(1), 11(16, 9-16), 12(1), 13(1), 14(12, 7-16), 15(1, 1-2). *Antenna*: Length about 0.33 of head; pigmentation light, shaft with a few scattered spicules. All hairs except 1 single; hair 1-A (2, 2-3) about 0.64 from base. *Thorax*: Integument glabrous. Apices of long hairs attenuate; stellate hairs with unequal, weakly barbed, spikelike branches. Prothorax: hair 0(28, 24-33), 1(2), 2(1, 1-2), 3(31, 27-36), 4(1), 5(1), 6(1), 7(2), 8(26, 20-29), 9(16, 15-21), 10(1), 11(2, 2-3), 12(1), 13(30, 29-37), 14(41, 38-45). Mesothorax: hair 1(22, 18-25), 2(1), 3(1), 4(1), 5(1), 6(4, 3-4), 7(1), 8(5, 4-6), 9(5, 4-7), 10(1), 11(1, 1-2), 12(1), 13(18, 13-20), 14(13, 11-15). Metathorax: hair 1(25, 23-37), 2(1), 3(16, 12-16), 4(3, 3-8), 5(16, 14-19), 6(1), 7(4, 3-4), 8(16, 15-16), 9(3, 3-4), 10(1), 11(1, 1-2), 12(1), 13(20, 18-23). *Abdomen*: Integument weakly spiculate, spicules simple, hair-like; stellate hairs as on thorax. Segment I: hair 1(18, 18-21), 2(17, 16-22), 3(1), 4(1), 5(16, 13-18), 6(3, 2-3), 7(1), 9(6, 4-6), 10(1), 11(16, 15-18), 13(16, 15-18). Segment II: hair 0(1), 1(20, 17-22), 2(20, 16-20), 3(1), 4(1), 5(16, 14-18), 6(2, 2-3), 7(12, 10-12), 8(1), 9(6, 6-9), 10(1), 11(1), 12(1), 13(24, 21-24). Segment III: hair 0(1), 1(18, 18-22), 2(17, 17-20), 3(1), 4(1), 5(16, 13-20), 6(1), 7(11, 10-13), 8(1), 9(14, 11-14), 10(1), 11(1), 12(1), 13(23, 21-28), 14(1). Segment IV: hair 0(1), 1(21, 19-24), 2(20, 16-22), 3(1), 4(1), 5(17, 16-19), 6(1, 1-2), 7(11, 10-13), 8(1), 9(15, 14-18), 10(1), 11(1), 12(1), 13(22, 18-25), 14(1). Segment V: hair 0(1), 1(21, 19-22), 2(20, 17-22), 3(1), 4(1), 5(17, 16-19), 6(2, 1-2), 7(10, 10-14), 8(1), 9(17, 14-20), 10(1), 11(1), 12(1), 13(22, 20-25), 14(1). Segment VI: hair 0(1), 1(21, 19-21), 2(22, 17-24), 3(1), 4(1), 5(16, 14-18), 6(1), 7(12, 10-14), 8(1), 9(16, 14-19), 10(1), 11(1), 12(1), 13(24, 22-26), 14(1). Segment VII: hair 0(1), 1(22, 20-24), 2(20, 18-22), 3(1, 1-2), 4(1), 5(18, 17-21), 6(9, 9-11), 7(1), 8(17, 14-19), 9(16, 14-17), 10(1), 11(1), 12(1), 13(24, 20-27), 14(1). *Segment VIII*: Comb scales in a single row, usually 16(14-16) in number; individual scale long, pointed apically, fringed nearly to tip. Hair 0(1), 1(24, 21-26), 2(1), 3(6, 5-7), 4(1), 5(24, 18-24), 14(1, 1-2). *Siphon*: Index about 3.3-3.67; integument moderately pigmented, with darker basal ring. Pecten extending to about 0.42-0.5, usually 18(16-22) teeth; individual tooth with basal denticles. Hair 1(4, 3-4), 2(1), 3-5 not visible, 6(1), 7(1), 8(2, 1-4), 9(1). *Anal Segment*: Saddle moderately pigmented, with a darker basal ring; caudal margin with spines of varying sizes. Gills subequal, more than 2.0 of saddle length. Hair 1(2), 2(4, 3-4), 3(1), 4a(2, 2-3), 4b(2), 4c(2), 4d(2, 1-2), 4e(1, 1-2).

SYSTEMATICS. *A. osornoi* is readily separated from its apparent nearest relatives, *marinkellei* and *leei*, by constant diagnostic features in all known stages. Immature stages and females are known only from elevations above 8,000 feet in Cundinamarca Province, Colombia, in the central part of the Cordillera Oriental. A female collected at 9,000 feet in the Sierra Nevada of the Cordillera de Merida in Venezuela [USNM] is undoubtedly *osornoi* and it seems very likely that the record of *quadri-vittatus* from Aragua in the Cordillera de la Costa (Cova Garcia, Sutil and Rausseo 1966) also pertains to this species. In the fair sample of material no striking variation is apparent except for 1 reared female from Cundinamarca Province (COB 37-13) where *osornoi* is sympatric with *marinkellei*. In this specimen a suggestion of possible hybridization or introgression of these 2 species is indicated in the *osornoi*-like ornamentation of the adult and in the resemblance of the immature stages to *marinkellei*. In this area of sympatry, the 2 species have not been collected together in the same bromeliad axils, suggesting an ecological barrier of some kind between them.

BIONOMICS. The known breeding sites of *osornoi* are epiphytic bromeliads at elevations above 8,000 feet. As in the case of *marinkellei*, several females have been taken, probably in biting-landing collections, at human bait.

DISTRIBUTION (fig.6). Colombia (Cordillera Oriental) and Venezuela (Cordillera de Merida and probably Cordillera de la Costa) at elevations of 8000-9000 ft. Material examined: 114 specimens; 11 ♂, 45 ♀, 22 pupae, 36 larvae; 22 individual rearings (20 larval, 2 incomplete).

COLOMBIA. *Cundinamarca*: Bogota, B.G. Amortegui, 5 ♀ [USNM]. Puerto Lievano and Bogota, 6 Aug 1935, B.G. Amortegui, 9 ♀ [USNM]. Rio San Francisco, 21 May 1942, W.H.W. Komp, 7 ♀ [USNM]; "Chorro de Padilla," elev. 8000 ft, 9 Feb 1965, E. Ruiz, 1 lp♂ (11-10), 1 lp♀ (11-11), 3 1 (COB 11), 12 ♀, 10 L (COB 650209); 25 Feb 1965, E. Ruiz, 2 1 (COB 14); 21 June 1965, J.A. Ochoa (COB 34), 3 lp♂ (34-18,93,94), 5 lp♀ (34-14-17,19), 2 lp (34-95,98), 1 ♂, 1 ♀; 14 July 1965, J.A. Ochoa (COB 36), 2 lp♂ (36-21,22), 1 lp♀ (36-20), (COB 37, type series), 3 lp♂ (37-11, 12,16), 3 lp♀ (37-10,17,18) [USNM, BM, UCLA].

VENEZUELA. *Aragua*: (Cova Garcia, Sutil and Rausseo 1966b:141). *Merida*: Sierra Nevada, elev. 9000 ft, Dec 1923, E.P. de Bellard, 1 ♀ [USNM].

31. *Aedes* (*Howardina*) *ecuadoriensis* Berlin, n.sp.

Figs.6,9,58

TYPES: Holotype ♀ (ECU 4), Leon River, Saraguro, Azuay, Ecuador, 5500 ft, adult collection, 22 Mar 1965, L.E. Pena G. [USNM]. Paratypes: 4 ♀ (ECU 4), same data as holotype [UCLA].

FEMALE. Wing: 2.88 mm. Proboscis: 2.25 mm. Forefemur: 1.62 mm. Abdomen: about 2.25 mm. Similar to *eleanorae*, with the following diagnostic differences. *Head*: Light scales on median and short orbital lines moderately broad, white; sides and venter with white scales. Erect scales dark. Palpus about 0.15 of proboscis; predominantly dark, with white scales on apex and base of segment 4. Mesal patch on torus white. *Thorax* (fig.9): Mesonotal light lines white and golden; inner dorsocentral line complete, narrow, white; outer dorsocentral line apparently complete, narrow, pale golden, extending from anterior margin to scutellum, a few anterior scales whitish; lateral marginal line short, whitish, extending from scutal angle to wingbase; scales on anterior promontory white. Light scales on median scutellar lobe broad, white, narrow and brown on lateral lobes. Scales on paratergite broad and white. *Apn* scales moderately broad, white; *ppn* with large upper and small lower scale patch; former with narrow white scales above, broad below; latter with broad white scales; other scale patches broad, white scaled, distributed as in the group. *Legs*: Forefemur dark scaled anteriorly, posterior surface predominantly creamy except for narrow longitudinal dark line from base to apex; midfemur and hindfemur mostly dark anteriorly except for a ventral white line to middle and a white spot at 0.67, posteriorly proximal 0.5 creamy, rest dark. Foretarsus with short incomplete white rings on segments 1,2; midtarsus with short white rings on 1-3; hindtarsus with broader white rings on 1-4. *Haltere*: Stem pale, knob predominantly white, a few brown scales dorsally. *Abdomen*: Basomedian tergal light scales dingy white on II-VII. Sternites with broad basal V-shaped patches of white scales; apical light scales distinct up to segment V.

MALE. Wing: 3.06 mm. Proboscis: 2.71 mm. Forefemur: 1.75 mm. Essentially similar to female in color. Palpus predominantly dark, basoventral parts of segments 4 and 5 white scaled.

MALE GENITALIA (fig.58). Diagnostic characters as in the key. Ninth tergite lobe prominent, with 6,7 moderate to strong bristles, inner markedly flattened and almost leaflike. Sidepiece length about 3.5 of median width. Clasper about 0.5 of sidepiece, with 2,3 subapical hairs; minute spicules in basal 0.5; spiniform short, 0.25

of clasper. Aedeagus short; dorsal sclerotization deeply emarginate, producing distinct lateral sclerotized lobes.

PUPA, LARVA unknown.

SYSTEMATICS. *A. ecuadoriensis* is readily separated from the apparently closely related *brevivittatus* by constant differences in mesonotal, pleural and tarsal markings. It is known only from 2 widely separated localities in northern and southern Ecuador in semi-arid areas (chaparral and high desert) at elevations between 5,000 and 6,000 feet, whereas *brevivittatus* is known at present only from intermediate localities with a range of elevations from 4,200 to nearly 11,000 feet, apparently always in humid forests.

BIONOMICS. Most of the known material of *ecuadoriensis* consists of females taken in biting-landing collections between the hours of 0600 and 1500. The immature stages will probably be found in bromeliads which undoubtedly contain water during the period of seasonal rainfall characteristic of the areas where the adults were collected.

DISTRIBUTION (fig.6). Ecuador (chaparral and high desert areas) at elevations of 5000-6000 ft. Material examined: 10 specimens; 2 ♂, 8 ♀; no individual rearings or immature stages.

ECUADOR. *Azuay*: Saraguro, Leon River, elev. 5500 ft, 22 Mar 1965, L.E. Pena G., 5 ♀ (ECU 4), type series [USNM, UCLA]. *Imbabura*: Ibarra, Taguando River, elev. 5400-5800 ft, 9 June 1965, L.E. Pena G., 2 ♂, 3 ♀ (ECU 25) [UCLA].

32. *Aedes* (Howardina) *brevivittatus* Berlin, n.sp.

Figs.6,9,58

TYPES: Holotype ♀, Zorrocucho, Azuay, Ecuador, 3500 m, date not specified, Levi-Castillo [USNM]. Allotype ♂ with associated genitalia slide, same data as holotype [USNM]. Paratypes: 8 ♀, same data as holotype [USNM, UCLA].

Aedes (Howardina) *quadrivittatus* in part of Dyar (1928:229); Edwards (1932:155); Lane (1939:100; 1953:713); Levi-Castillo (1953:40); Stone, Knight and Starcke (1959:174).

FEMALE. Wing: 5.04 mm. Proboscis: 3.27 mm. Forefemur: 2.79 mm. Abdomen: about 4.55 mm. Similar to *eleanorae*, differing in larger size and in the following. *Head*: Light scales of median and short orbital lines creamy; light scales on sides and venter whitish. Erect scales predominantly brown, a few middle ones paler. Palpus about 0.14 of proboscis; predominantly dark, with white scales on apex and mesal side of segment 4. Mesal patch on torus white. *Thorax* (fig.9): All mesonotal light lines creamy to pale golden; inner dorsocentral line slightly broadened on anterior 0.5, gradually narrowing caudad; outer dorsocentral line shorter, from anterior 0.25 to scutellum; lateral marginal line longer, from anterior promontory to wingbase; scales on anterior promontory golden. Light scales on median scutellar lobe narrow, white; lateral lobes with narrow, brown scales. Scales on paratergite broad, dingy white. *Apn* scales broad, dingy white, a few anterior ones narrower; *ppn* with only an upper patch of predominantly narrow, creamy scales, a few broader ones below; other pleural patches with broad white scales, distributed as in the group. *Legs*: Forefemur dark brown anteriorly, posteriorly proximal 0.5 predominantly creamy extending distally as a narrow creamy line, rest dark; midfemur mostly dark brown anteriorly except for a few basal creamy scales and a white spot at 0.67, posteriorly prox-

imal 0.5 creamy, extending distally as a creamy line, rest dark; hindfemur creamy to 0.75 anteriorly, 0.67 posteriorly, rest dark scaled. Foretarsus with a few white scales on segments 1,2; midtarsus with short incomplete white rings on 1-3; hindtarsus with short white rings on 1-4. *Haltere*: Stem pale, knob predominantly dark, fringe scales whitish. *Abdomen*: Basal tergal light bands creamy to V, white on VI,VII. Sternites with broad basal patches, creamy basally and white on sides; apical creamy to white scales distinct up to segment V.

MALE. Wing: 5.6 mm. Proboscis: 3.45 mm. Forefemur: 2.37 mm. Essentially similar to female in color. Palpus predominantly dark, basoventral parts of segments 4 and 5 white scaled.

MALE GENITALIA (fig.58). As figured; diagnostic characters as in the key. Ninth tergite lobe prominent, with 6,7 strong bristles. Sidepiece length about 2.5 of median width. Clasper about 0.5 of sidepiece, with 1,2 subapical hairs; spiniform moderate, about 0.33 of clasper. Aedeagus subquadrate; dorsal sclerotization deeply emarginate, producing distinct lateral lobes.

PUPA, LARVA unknown.

SYSTEMATICS. *A. brevivittatus* is apparently closely related to *ecuadoriensis* with which it is broadly sympatric in Ecuador but from which it seems to be isolated by a strong ecological barrier. While *ecuadoriensis* is known only from semi-arid localities at elevations of 5,000 to 6,000 feet, *brevivittatus* has been collected only in humid forests at elevations from 4,200 to nearly 11,000 feet, apparently only on the western slopes of the Andes.

BIONOMICS. The immature stages of *brevivittatus* will undoubtedly be found in epiphytic and/or terrestrial bromeliads. The present collections consist mostly of females taken biting-landing on humans between the hours of 1000 and 1800.

DISTRIBUTION (fig.6). Humid forests on western slopes of Andes in Ecuador at elevations of 4200-11,000 ft. Material examined: 25 specimens; 8 ♂, 17 ♀; no individual rearings or immature stages.

ECUADOR. *Azuay*: Cuenca, Caserio Tinajillas, elev. 10,000 ft, 18-21 Mar 1965, L.E. Pena G., 7 ♂, 7 ♀ (ECU 3) [UCLA]. *Zorrocucho*, elev. 3500 m, Levi-Castillo, 1 ♂, 9 ♀, type series [USNM, UCLA]. *Canar*: (Levi-Castillo 1953:40). *Pichincha*: Santo Domingo, Tandapi, elev. 4400-5400 ft, 20-21 June 1965, L.E. Pena G., 1 ♀ (ECU 27) [UCLA].

Aurivittatus Group

FEMALES. *Head*: Median light line on vertex with narrow scales. Proboscis distinctly longer than forefemur. Torus with restricted mesal scale patch. *Thorax*: Mesonotal light lines usually creamy to golden; inner dorsocentral line complete; outer dorsocentral line either complete or not reaching anterior margin, subparallel to inner; lateral marginal line continuous; scales on anterior promontory pale golden. Antealar area above paratergite with golden scales. Paratergite with a moderate scale patch extending entire sclerite length. Upper *ppn* entirely covered with light scales; upper *stp* patch quadrate. *Legs*: Distal white spot on anterior surface of midfemur distinct, absent on hindfemur. Tibiae completely dark. *Wing*: Remigium with white scales. *Abdomen*: Basomedian tergal light markings absent.

MALES. Palpus with basomedian light scales on segments 4 and 5.

MALE GENITALIA. Lobe of tergite IX distinct, with 5,6 strong bristles. Sidepieces separated at base by a distance less than width of aedeagus; without any indication of lobes on tergomesal or sternomesal margins. Claspette represented by a

conical tubercle. Aedeagus shorter than proctiger; apex slightly emarginate, producing lateral lobes.

PUPAE and LARVAE unknown.

DISCUSSION. The *Aurivittatus* Group is recognized here for the nominate form, *vanemdeni* and *martinezi* on the basis of the presence of pale scales on the remigium. The immature stages are unknown for the group and I have not seen any males. The group is doubtfully distinct from the *Eleanorae* Group and may have to be merged with it if the immature stages prove to be similar. Members of this group have been occasionally misidentified as *sexlineatus* in the past.

The group occupies the southernmost portion of the distribution of the section. *A. aurivittatus* and *vanemdeni* have been found only in Bolivia, at moderate elevations in the Amazon basin; *martinezi* is known at moderate elevations in the Amazon basin in Bolivia and from northern Argentina at an elevation of about 5,000 feet and is one of the 2 members of the section reported from the La Plata drainage (fig.5).

33. *Aedes* (*Howardina*) *aurivittatus* Cerqueira

Figs.5,9

1943. *Aedes* (*Howardina*) *aurivittatus* Cerqueira, 1943a:7-8. TYPE: Holotype ♀, Pampagrande, Florida, Santa Cruz, Bolivia, Feb 1940 [IOC].

Aedes (*Howardina*) *aurivittatus* of Cerqueira (1943b:33); Del Ponte, Castro and Garcia (1951:240); Lane (1953:711); Stone, Knight and Starcke (1959:173); in part of Martinez, Prosen and Carcavallo (1964:53-58); Prosen, Carcavallo and Martinez (1964:103); Forattini (1965:461); Stone (1967:208).

FEMALE. Wing: 3.24 mm. Proboscis: 2.16 mm. Forefemur: 1.89 mm. Abdomen: about 2.88 mm. *Head*: Light decumbent scales on head white. Erect scales extending to vertex, light brown on occiput. Palpus about 0.16 of proboscis; white scales restricted to base and apex of segment 4. Mesal scale patch on torus silvery white. *Thorax* (fig.9): Mesonotal light lines creamy to pale golden; inner dorsocentral line complete, extending from anterior margin to scutellum; outer dorsocentral line complete, merging with lateral marginal line at level of humeral bristles; lateral marginal line long, extending from humeral bristles to wingbase. Median scutellar lobe with broad dark scales laterally and moderately broad creamy scales from base to apex in middle; lateral lobe with a few narrow creamy scales. Paratergite with moderately broad white scales. Scales on *apn* predominantly broad and white, a few anterior ones narrower; *ppn* with large upper and small lower patches, former predominantly with narrow scales except for lower broader ones, latter with broad white scales; *psp* with a few broad white scales restricted to posterior part of bristles; other patches pure white, distributed as in the group. *Legs*: Forefemur mostly dark except for a few white scales at base anteriorly and a creamy longitudinal line posteriorly; midfemur predominantly dark anteriorly except for a narrow mesal line from base terminating in a distinct silvery spot at 0.67, posteriorly proximal 0.5 creamy, rest dark; hindfemur mostly creamy to 0.67 on both sides, rest dark scaled. Foretarsus and midtarsus with a few white scales on segment 1; hindtarsus with moderately broad white rings on segments 1-3. *Haltere*: Stem pale, knob brown scaled basally, fringe scales whitish. *Abdomen*: Sternites with broad V-shaped basal white patches; median apical white scales few, present up to segment V.

MALE. Not seen; according to the description of Martinez, Prosen and Carcavallo (1964:53-58), essentially similar to female as described above.

MALE GENITALIA. Diagnostic characters as in the key. Ninth tergite lobe prominent, with 6 strong bristles. Sidepiece length about 3.0 median width. Clasper about 0.5 of sidepiece, with 1 subapical hair; spiniform long, about 0.5 of clasper. Aedeagus shorter than proctiger; dorsal sclerotization slightly emarginate, producing lateral lobes.

PUPA, LARVA unknown.

SYSTEMATICS. The 3 females of *aurivittatus* I have examined are readily separated from *martinezi* by the diagnostic characters mentioned above. This species appears to be restricted to moderate elevations in the upper parts of the Amazon drainage in Bolivia. The record of *aurivittatus* from La Caldera (Salta), Argentina, is probably erroneous and based on the closely related *martinezi* which has been collected in the same locality.

BIONOMICS. The immature stages are unknown but should be found in the axils of epiphytic and/or terrestrial bromeliads, the only known breeding sites of the members of the Sexlineatus Section. Females of *aurivittatus* are evidently at least occasionally attracted to humans, presumably in the daytime.

DISTRIBUTION (fig.5). Bolivia (upper Amazon drainage) at moderate elevations. Material examined: 3 specimens; 3 ♀; no individual rearings or immature stages.

BOLIVIA. *Cochabamba*: Chapare, 27 Apr 1944, 1 ♀ [USNM]. *Santa Cruz*: Florida, Feb 1940, N.L. Cerqueira, 2 ♀ paratypes [USNM].

34. *Aedes* (Howardina) *martinezi* Berlin, n.sp.

Figs.5,9

TYPE: Holotype ♀ (ARG-1), La Caldera, Salta, Argentina, 27 Mar 1966, A. Martinez [USNM]. Paratypes: 30 ♀, same data as holotype [USNM, BM, UCLA]. This species is dedicated to Dr. A. Martinez for his contributions to the study of neotropical mosquitoes.

Aedes (Howardina) *aurivittatus* in part of Martinez and Prosen (1955:25-27); Castro, Garcia and Bressanello (1959:550).

FEMALE. Wing: 3.42 mm. Proboscis: 2.36 mm. Forefemur: 2.19 mm. Abdomen: 2.91 mm. Essentially similar to *aurivittatus*, differing apparently only in the following. *Head*: Light decumbent scales dull creamy. Erect scales on occiput largely brownish, a few darker. *Thorax* (fig.9): Mesonotal light lines pale golden; outer dorsocentral line shorter, arising at anterior 0.25; lateral marginal line long, from side of anterior promontory to wingbase. Lateral scutellar lobes with a few narrow dark scales.

MALE, PUPA, LARVA unknown.

SYSTEMATICS. *A. martinezi* has been confused in the past with *aurivittatus* from which it is clearly differentiated by the diagnostic characters mentioned above which are remarkably constant in the small type series. Apparently *martinezi* extends from moderate elevations in the Amazon basin in Bolivia to the upper part of the La Plata drainage in northern Argentina.

BIONOMICS. The immature stages are unknown but will probably be found in the axils of bromeliads. The adults have been captured biting and landing on humans during the day at elevations of about 5,000 feet.

DISTRIBUTION (fig.5). Bolivia (upper Amazon drainage) and Argentina (upper La Plata drainage), at moderate to high elevations. Material examined: 32 specimens; 32 ♀, no individual rearings or immature stages.

ARGENTINA. *Salta*: La Caldera, 3.0 mi before mountain pass Sta. Laura, elev. 5000 ft, 27 Mar 1966, A. Martinez, 31 ♀ (ARG-1, type series) [USNM, BM, UCLA].

BOLIVIA. *Cochabamba*: Chimore, 30 Apr 1944, 1 ♀ [USNM].

35. *Aedes* (Howardina) *vanemdeni* Martini

Figs.5,9

1931. *Aedes vanemdeni* Martini, 1931:208-209. TYPE: Lectotype ♂, Yungas de Coroico (La Paz), Bolivia, elev. 1000 m [BM; selection of Mattingly 1955:31].

Aedes (Howardina) *vanemdeni* of Lane (1939:101); Martinez (1950:39); Del Ponte, Castro and Garcia (1951:240); Lane (1953:716); Martinez and Prosen (1953:28,30; 1955:32); Castro, Garcia and Bressanello (1959:550); Stone, Knight and Starcke (1959:174); Prosen, Carcavallo and Martinez (1964:105).

FEMALE. Not seen.

MALE. Essentially similar to *aurivittatus*, differing apparently only in the following (fig.9). Lateral marginal line short, not connected to outer dorsocentral line at level of humeral bristles and extending from scutal angle to wingbase. Forefemur and midfemur with a distinct white spot anteriorly at distal 0.67. Foretarsus and midtarsus with white scales on segments 1-3; hindtarsus with white ring only on segment 1; rest dark scaled. *Haltere*: Stem pale, knob entirely white scaled.

MALE GENITALIA. Ninth tergite lobe distinct, with 5 strong bristles. Sidepiece length about 3.0 of median width. Clasper and spiniform as in *aurivittatus*.

PUPA and LARVA unknown.

SYSTEMATICS. *A. vanemdeni* is readily differentiated from other members of the *Aurivittatus* Group by the distribution of the tarsal white markings. The male genitalia appear to be similar to *aurivittatus*. *A. vanemdeni* is known only by the ♂ (lectotype) and ♀ of the original type series from moderate elevations in the Amazon basin in Bolivia.

BIONOMICS. The unknown immature stages will probably be found in bromeliad axils. Females are presumably at least occasionally attracted to man.

DISTRIBUTION. Bolivia (fig.5). Material examined: ♂ lectotype examined by J.N. Belkin [BM].

REFERENCES CITED

- Aitken, T.H.G.
1960. A survey of Trinidadian arthropods for natural viral infections (August 1953 to December 1958). *Mosquito News* 20:1-10.
- Anduze, P.J.
1941. Lista provisional de los zancudos hematofagos de Venezuela (Diptera: Culicidae). *Bol. Entomol. Venezolana* 1:6-18.
1943. Estudios de entomologia medica en el estado Merida-Venezuela. *Bol. Entomol. Venezolana* 2:189-196.
1947. Contribucion al estudio de los vectores de la fiebre amarilla en Venezuela. *Acad. Cien. Fis. Mat. Natur., Caracas, Bol.* 10:331-373.
- Antunes, P.C.A.
1937a. Informe sobre una investigacion entomologica realizada en Colombia. Colombia, Univ. Nac., Bogota. Fac. Med., Rev. 6:3-29.
1937b. Informe sobre una investigacion entomologica realizada en Colombia. Colombia, Univ. Nac., Bogota. Fac. Med., Rev. 6:65-87.
- Arnett, R.H.
1949. Notes on the distribution, habits, and habitats of some Panama culicines (Diptera: Culicidae). *N.Y. Entomol. Soc., J.* 57:233-251.
1950. Notes on the distribution, habits, and habitats of some Panama culicines (Diptera: Culicidae). *N.Y. Entomol. Soc., J.* 58:99-115.
- Bates, M.
1944. Observations on the distribution of diurnal mosquitoes in a tropical forest. *Ecology* 25:159-170.
1945. Observations on climate and seasonal distribution of mosquitoes in Eastern Colombia. *J. Anim. Ecol.* 14:17-25.
1949. The natural history of mosquitoes. New York, MacMillan. 379 p.
- Belem Virus Lab.
1964. Annual Report. Belem, Para, Brazil. 133 p.
- Belkin, J.N.
1955. The *Tripteroides caledonica* complex of mosquitoes in Melanesia (Diptera: Culicidae). *Pacific Sci.* 9:221-246.
1962. The mosquitoes of the South Pacific. v.1. Berkeley, U. Calif. Press. 608 p.
1968. Mosquito Studies (Diptera, Culicidae). IX. The type specimens of New World mosquitoes in European museums. *Amer. Entomol. Inst., Contrib.* 3(4):1-69.
- Belkin, J.N., C.L. Hogue, P. Galindo, T.H.G. Aitken, R.X. Schick and W.A. Powder
1965. Mosquito Studies (Diptera, Culicidae). II. Methods for the collection, rearing and preservation of mosquitoes. *Amer. Entomol. Inst., Contrib.* 1(2):19-78.
- Belkin, J.N., R.X. Schick, P. Galindo and T.H.G. Aitken
1965. Mosquito Studies (Diptera, Culicidae). I. A project for a systematic study of the mosquitoes of Middle America. *Amer. Entomol. Inst., Contrib.* 1(2):1-17.
- Belkin, J.N., R.X. Schick and S.J. Heinemann
1965. Mosquito Studies (Diptera, Culicidae). V. Mosquitoes originally described from Middle America. *Amer. Entomol. Inst., Contrib.* 1(5):1-95.
- Blanchard, R.
1905. Les moustiques. Histoire naturelle et medicale. Paris, F.R. de Rudeval. 673 p.

Blanton, F.S. and E.L. Peyton

1958. Notes and distribution of *Aedes* mosquitoes in Panama based on a three year light trap survey. Mosquito News 18:30-33.

Bonne, C. and J. Bonne-Wepster

1925. Mosquitoes of Surinam. Roy. Colon. Inst., Amsterdam, Afd. Trop. Hyg. 13:1-558.

Bonne-Wepster, J. and C. Bonne

1920. Diagnoses of new mosquitoes from Surinam, with a note on synonymy. Insecutor Inscitiae Mens. 7:165-180.

Boshell-Manrique, J. and E. Osorno-Mesa

1944. Observations on the epidemiology of the jungle yellow fever in Santander and Boyaca, Colombia, September 1941 to April 1942. Amer. J. Hyg. 40:170-181.

Bugher, J.C., J. Boshell-Manrique, M. Roca-Garcia and E. Osorno-Mesa

1944. Epidemiology of jungle yellow fever in Eastern Colombia. Amer. J. Hyg. 39:16-51.

Carpenter, S.J., P. Galindo and H. Trapido

1952. Forest mosquito studies in an endemic yellow fever area in Panama. Mosquito News 12:156-164.

Carpenter, S.J. and E.L. Peyton

1952. Mosquito studies in Panama Canal Zone during 1949 and 1950 (Diptera, Culicidae). Amer. Midland Natur. 48:673-682.

Castro, M., M. Garcia and M.D. Bressanello

1959. Diptera Culicidae Culicinae. Primeras Jornadas Entomoepidemiol. Argent., Buenos Aires, p.547-562.

Causey, O.R. and H.W. Kumm

1948. Dispersion of forest mosquitoes in Brazil. Preliminary studies. Amer. J. Trop. Med. 28:469-480.

Causey, O.R., H.W. Kumm and H.W. Laemmert

1950. Dispersion of forest mosquitoes in Brazil. Further studies. Amer. J. Trop. Med. 30:301-312.

Causey, O.R. and G.V. Dos Santos

1949. Diurnal mosquitoes in an area of small residual forests in Brazil. Entomol. Soc. Amer., Ann. 42:471-482.

Cerqueira, N.L.

1943a. Algunas especies novas da Bolivia, e referencia a tres especies de *Haemagogus* (Diptera, Culicidae). Inst. Oswaldo Cruz, Rio de Janeiro, Mem. 39:1-14.

1943b. Lista dos mosquitos da Bolivia (Diptera, Culicidae). Inst. Oswaldo Cruz, Rio de Janeiro, Mem. 39:15-36.

Coquillett, D.W.

1902. Three new species of *Culex*. Can. Entomol. 34:292-293.

1905. New Culicidae from West Indies and Central America. Entomol. Soc. Wash., Proc. 7:182-186.

1906a. Five new Culicidae from the West Indies. Can. Entomol. 38:60-62.

1906b. A classification of the mosquitoes of North and Middle America. U.S. Bur. Entomol., B. Tech. Ser. 11:1-31.

1910. The type species of the North American Genera of Diptera. U.S. Nat. Mus., Proc. 37:499-647.

Cova Garcia, P., E. Sutil and J.A. Rausseo

1966a. Mosquitos (Culicinos) de Venezuela, v.1. Caracas, Min. Sanid. Asistencia

- Soc. 410 p.
1966b. Mosquitos (Culicinos) de Venezuela, v.2. Caracas, Min. Sanid. Asistencia Soc. 406 p.
- Davis, N.C. and R.C. Shannon
1931. Further attempts to transmit yellow fever with mosquitoes of South America. Amer. J. Hyg. 14:715-722.
- Del Ponte, E., M.P. Castro and M. Garcia
1951. Clava para las especies de *Psorophora* y *Aedes* de la Argentina y comarcas vecinas. Diagnosis de *Aedes* (O.) *raymondi* n.sp. (Diptera, Culicidae). Soc. Cien. Argent., An. 151:228-243.
- Diaz Najera, A.
1966a. *Aedes* de Mexico. Descripcion de una nueva especie del subgenero *Howardina* (Diptera, Culicidae). Rev. Invest. Salud. Publ. (Mex.) 24:331-344.
1966b. Mosquitos tropicales de Mexico. Rev. Invest. Salud. Publ. (Mex.) 26:57-64.
- Dyar, H.G.
1905a. Remarks on genitalic genera in the Culicidae. Entomol. Soc. Wash., Proc. 7:42-49.
1905b. A synoptic table of North American mosquito larvae. N.Y. Entomol. Soc., J. 13:22-26.
1905c. Brief notes on mosquito larvae. N.Y. Entomol. Soc., J. 13:26-29.
1906. Illustrations of mosquito larvae. Entomol. Soc. Wash., Proc. 8:15-21.
1918. The male genitalia of *Aedes* as indicative of natural affinities. Insecutor Inscitiae Mens. 6:71-86.
1920. The Classification of American *Aedes*. Insecutor Inscitiae Mens. 8:103-106.
1925. The mosquitoes of Panama. Insecutor Inscitiae Mens. 13:101-195.
1928. The mosquitoes of the Americas. Washington, Carnegie Inst. (Publication 387). 616 p.
- Dyar, H.G. and F. Knab
1906a. Notes on some American mosquitoes with description of new species. Biol. Soc. Wash., Proc. 19:159-172.
1906b. The larvae of Culicidae classified as independent organisms. N.Y. Entomol. Soc., J. 14:169-230.
1907. Description of some American mosquitoes. N.Y. Entomol. Soc., J. 15:9-13.
1913. Three new Neotropical mosquitoes. Insecutor Inscitiae Mens. 1:76-78.
1919. New species of tropical American mosquitoes. Insecutor Inscitiae Mens. 7:1-9.
- Dyar, H.G. and M. Nunez Tovar
1927. Notes on biting flies from Venezuela. Insecutor Inscitiae Mens. 14:152-154.
- Edwards, F.W.
1932. Diptera fam. Culicidae. In P. Wytsman, Genera Insectorum, Brussels, Desmet-Verteneuil, Fasc. 194. 258 p.
- Fauran, P.
1961. Catalogue annote des Culicides signales en Guyane Francaise. Inst. Pasteur Guyane Franc. Inini, Arch. Publication 465. 66 p.
- Floch, H. and E. Abonnenc
1942a. Especies de moustiques signalees pour la premiere fois en Guyane Francaise. Inst. Pasteur Guyane Ter. Inini, Publication 41. 6 p.
1942b. Catalogue et distribution geographique des moustiques de la Guyane Francaise actuellement connus (1). Inst. Pasteur Guyane Ter. Inini, Publication 43. 10 p.

1944. Culicides et Ixodides Guyanais. Moustiques signales pour la premiere fois et presence de *Ornithodoros talaje* en Guyane francaise. Inst. Pasteur Guyane Ter. Inini, Publication 86. 6 p.
1945. Les Moustiques de la Guadeloupe (II). Les Genres *Megarhinus*, *Aedes*, *Culex*, *Deinocerites*, *Mansonia* et *Wyeomyia*. Inst. Pasteur Guyane Ter. Inini, Publication 110. 48 p.
1947. Distribution des culicines des genres autres que la genre *Culex*, en Guyane Francaise. Inst. Pasteur Guyane Ter. Inini, Publication 148. 12 p.
- Floch, H. and P. Fauran
1954. Lutte antipaludique et lutte antiamarile en Guyane francaise. Inst. Pasteur Guyane Franc. Inini, Arch. Publication 322. 67 p.
- Forattini, O.P.
1965. Entomologia Medica. v.2. Sao Paulo, Univ. 506 p.
- Galindo, P.
1964. Ecology of Arthropod-borne viruses in Panama. Gorgas Mem. Lab., Annu. Progr. Rep. 130 p.
- Galindo, P., S.J. Carpenter and H. Trapido
1951. Ecological observations on forest mosquitoes of an endemic area in Panama. Amer. J. Trop. Med. 31:98-137.
1955. A contribution to the ecology and biology of treehole breeding mosquitoes of Panama. Entomol. Soc. Amer., Ann. 48:158-164.
- Galindo, P. and H. Trapido
1957. Forest mosquitoes associated with sylvan yellow fever in Nicaragua. Amer. J. Trop. Med. Hyg. 6:145-152.
- Galindo, P., H. Trapido and S.J. Carpenter
1950. Observations on diurnal forest mosquitoes in relation to sylvan yellow fever in Panama. Amer. J. Trop. Med. 30:533-574.
- Gerry, B.I.
1932. Morphological studies of the female genitalia of Cuban mosquitoes. Entomol. Soc. Amer., Ann. 25:31-64.
- Giles, G.M.
1902. A handbook of the Gnats or Mosquitoes. London, John Dale and Danielsson. 530 p.
- Gowdey, C.C.
1926. Catalogus Insectorum Jamaicensis. Jamaica. Dept. Agri., Ent. Bull. 4:1-114.
- Grabham, M.
1906. Notes on some mosquitoes from Newcastle, Jamaica. Can. Entomol. 38: 167-173.
1907. Notes on some mosquitoes from Jamaica, West Indies. Can. Entomol. 39: 25-26.
- Hill, R.B. and C.M. Hill
1948. The mosquitoes of Jamaica. Inst. Jamaica, B., Sci. Ser. 4. 60 p.
- Horsfall, W.R.
1955. Mosquitoes, their bionomics and relation to disease. N.Y., Ronald Press. 723 p.
- Howard, L.O., H.G. Dyar and F. Knab
1912. The mosquitoes of North and Central America and the West Indies. v.1. Washington, Carnegie Inst. (Publication 159). 520 p.
1917. The mosquitoes of North and Central America and the West Indies. v.4. Washington, Carnegie Inst. (Publication 159). p. 525-1064.

Johnson, C.W.

1919. A revised list of Diptera of Jamaica. Amer. Mus. Nat. Hist., Bull. 41:421-449.

Knight, K.L. and E.N. Marks

1952. An annotated checklist of the mosquitoes of the subgenus *Finlaya*, genus *Aedes*. U.S. Nat. Mus., Proc. 101:513-574.

Komp, W.H.W.

- 1936a. An annotated list of the mosquitoes found in the vicinity of an endemic focus of yellow fever in the Republic of Colombia. Entomol. Soc. Wash., Proc. 38:57-70.

- 1936b. The male and larva of *Aedes dominicii* Rangel & Romero Sierra, and the male of *Aedes pseudodominicii* sp.nov., representatives of a new subgenus (*Soperia*) of the genus *Aedes*, from Colombia. Entomol. Soc. Wash., Proc. 38:71-75.

1956. Notes on mosquitoes from an area of endemic yellow fever in Colombia. Entomol. Soc. Wash., Proc. 58:37-42.

Kumm, H.W. and W.H.W. Komp

1941. *Aedes (Howardina) allotecnion*, a new species of *Aedes* from Costa Rica, and description of the larva, adult and male terminalia of *Aedes quadrivittatus* (Coq). Entomol. Soc. Wash., Proc. 43:17-25.

Kumm, H.W., W.H.W. Komp and H. Ruiz

1940. The mosquitoes of Costa Rica. Amer. J. Trop. Med. 20:385-422.

Kumm, H.W. and O. Novis

1938. Mosquito studies on the Ilha de Marajo, Para, Brazil. Amer. J. Hyg. 27:498-515.

Kumm, H.W. and H. Zuniga

1942. Mosquitoes of El Salvador. Amer. J. Trop. Med. 22:399-415.

van der Kuyp, E.

1954. Mosquitoes of Netherlands Antilles and their hygienic importance. Stud. Fauna Curacao Caribbean Islands 5:37-114.

Lane, J.

- 1936a. Notas sobre investigacoes entomologicas em localidades onde houve febre amarella sylvestre em Sao Paulo. Arch. Hyg. Saude Pub., Sao Paulo 2:127-133.

- 1936b. Notas sobre culicideos de Matto Grosso. Mus. Paulista, Sao Paulo, Rev. 20:173-206.

1939. Catalogo dos mosquitos neotropicos. Sao Paulo, Clube Zool. Brasil. 218 p.

1949. Zoogeography of the Culicidae in the world. Mus. Paranaense, Curitiba, Rev. 7:247-263.

1951. Synonymy of Neotropical Culicidae. Entomol. Soc. Wash., Proc. 53:333-336.

1953. Neotropical Culicidae, v.2. Sao Paulo, Univ. p.554-1112.

Levi-Castillo, R.

- 1952a. Estudios epidemiologicos sobre la Fiebre Amarilla selvatica en las Provincias de Manabi y esmeraldas de la zona costera de la Republica del Ecuador. Rev. Kuba Med. Trop. 8(10,11 y 12):76-81.

- 1952b. Vorlaufige liste der stechmucken (Uranotaeniini, Toxorhynchitini, Culicini, Aedini, and Sabethini) aus Ecuador (Diptera, Culicidae). Z. Tropenmed. Parasitol. 3(4):552-559.

1953. Lista provisional y distribucion de los mosquitos culicinos en el Ecuador. Rev. Ecuador. Entomol. Parasitol. 1(1):34-45.

Lima, A. de Costa

1930. Sobre os mosquitos que se craim em buracos de arvores. Inst. Oswaldo Cruz, Rio de Janeiro, Mem. 23:255-260.

Lutz, A.

1904. Catalogo dos culicideos Brasileiros e Sul-Americanos. In Bourroul, C. Mosquitos do Brasil. 16 p.

1905. Novas especies do Mosquitos do Brasil. Imprensa Med., Sao Paulo 13:65-70.

Martinez, A.F.

1950. Algunos Culicidae nuevos o poco conocidos para las entomofaunas de Argentina, Bolivia y Paraguay. Mision Estud. Patol. Reg. Argent. 21:33-41.

Martinez, A.F., R.U. Carcavallo and A.F. Prosen

1960. Una nueva especie de Culicidae de Bolivia. Univ. Buenos Aires, Fac. Cien. Med., Cat. Microbiol. Parasitol., Rev. 28:25-29.

Martinez, A. and A.F. Prosen

1953. Nuevos Culicidos para las entomofaunas de Argentina, Bolivia y Paraguay. Mision Estud. Patol. Reg. Argent. 24:27-32.

1955. Las especies de *Aedes* (*Howardina*) de Argentina y Bolivia (Diptera, Culicidae). Mision Estud. Patol. Reg. Argent. 26:21-41.

1959. Nuevos culicidos para las entomofaunas de Argentina, Bolivia y Paraguay. Primeras Jornadas Entomoepidemiol. Argent., Buenos Aires, p.603-607.

Martinez, A., A.F. Prosen and R.U. Carcavallo

1964. El alotipo macho de *Aedes* (*Howardina*) *aurivittatus* Cerquiera. Inst. Med. Reg., An. 6(1/2):53-58.

Martini, E.C.W.

1931. Ueber einige sudamerikanische Culiciden. Rev. Entomol. 1:199-219.

1935. Los mosquitos de Mexico. Mex. Dep. Salubr., Bol. Tec. (A) 1. 65 p.

Matheson, R.

1950. Medical Entomology. ed.2. Ithaca, N.Y., Comstock. 612 p.

Mattingly, P.F.

1955. Mosquitoes (Diptera: Culicidae) from the Tropical Institute at Hamburg. Roy. Entomol. Soc. Lond., Proc. (B) 24:27-33.

Montchadsky, A.S. and I. Garcia Avila

1966. Las larvas de los mosquitos (Diptera, Culicidae) de Cuba, su biologia y determinacion. Poeyana (A) 28. 92 p.

Peryassu, A.G.

1908. Os culicidos do Brasil. Rio de Janeiro, Inst. Manguinhos. 407 p.

Peyton, E.L., P. Galindo and F.L. Blanton

1958. Pictorial keys to genera of Panama mosquitoes. Mosquito News 15:85-100.

Picado, C.

1913. Les bromeliacees epiphytes considerees comme milieu biologique. B. Biol. France Belg. (7) 47:215-360.

Porter, J.R.

1967. A checklist of the mosquitoes of the Greater Antilles and the Bahama and Virgin Islands. Mosquito News 27:35-41.

Prosen, A.F., R.U. Carcavallo and A. Martinez

1964. Culicidae de Bolivia. Inst. Med. Reg., An. 6(1/2):59-124.

Reyes, P.

1955. Lista de mosquitos de Colombia, S.A. (Diptera, Culicidae). Soc. Biol. Bogota, An. 7(2):46-94.

Root, F.M.

1927. Notes on the mosquito fauna of the Republic of Haiti. Amer. J. Hyg. 7: 463-469.

Senevet, G.

1936. Les moustiques de la Martinique. Inst. Pasteur Algerie, Arch. 14:123-134.

1938. Les moustiques de la Guadeloupe. Inst. Pasteur Algerie, Arch. 16:176-190.

Senevet, G. and L. Quievreux

1941. Les moustiques de la Martinique (2e memoire). Inst. Pasteur Algerie, Arch. 19:248-264.

Shannon, R.C.

- 1931a. The environment and behavior of some Brazilian mosquitoes. Entomol. Soc. Wash., Proc. 33:1-27.

- 1931b. On the classification of Brazilian Culicidae with special reference to those capable of harboring the yellow fever virus. Entomol. Soc. Wash., Proc. 33: 125-164.

Soper, F.L., H. Penna, E. Cordoso, J. Serafim, M. Frobisher and J. Pinheiroz

1933. Yellow fever without *Aedes aegypti*. Study of a rural epidemic in the Valle do Chanaan, Espirito Santo, Brazil, 1932. Amer. J. Hyg. 18:555-587.

Spielman, A. and A.E. Weyer

1965. Description of *Aedes (Howardina) albonotatus* (Coquillett), a common domestic mosquito from the Bahamas. Mosquito News 25:339-343.

Stone, A.

1963. A Synoptic Catalog of the Mosquitoes of the World (Diptera, Culicidae). Supp. II. Entomol. Soc. Wash., Proc. 65:117-140.

1967. A Synoptic Catalog of the Mosquitoes of the World (Diptera, Culicidae). Supp. III. Entomol. Soc. Wash., Proc. 69:197-224.

Stone, A. and K.L. Knight

1956. Type specimens of mosquitoes in the United States National Museum: II, The genus *Aedes* (Diptera, Culicidae). Wash. Acad. Sci., J. 14:213-228.

Stone, A., K.L. Knight and M. Starcke

1959. A Synoptic Catalog of the Mosquitoes of the World (Diptera, Culicidae). Wash., Entomol. Soc. Amer. (Thomas Say Found. Publication 6). 358 p.

Suarez, O.M. and P. Cova Garcia

1961. Estudio morfologico de *Aedes (H.) ioliota* Dyar and Knab, 1913. Rev. Brasil. Entomol. 10:17-24.

Surcouf, J. and R. Gonzalez-Rincones

1911. Essai sur les Dipteres vulnerants du Venezuela. Premiere Partie. Dipteres Nematoceres vulnerants. Paris, Maloine. 320 p.

1912. Dipteres piqueurs et suceurs de sang actuellement connus, de la Republique de Venezuela. Arch. Parasitol. Paris 15:248-314.

Theobald, F.V.

1901. A monograph of the Culicidae or mosquitoes. v.1. London, Brit. Mus. (Natur. Hist.). 424 p.

- 1903a. A monograph of the Culicidae or mosquitoes. v.3. London, Brit. Mus. (Natur. Hist.). 359 p.

- 1903b. Notes on the genus "*Stegomyia*" (Theobald), and its distribution. J. Trop. Med. 6:237-239.

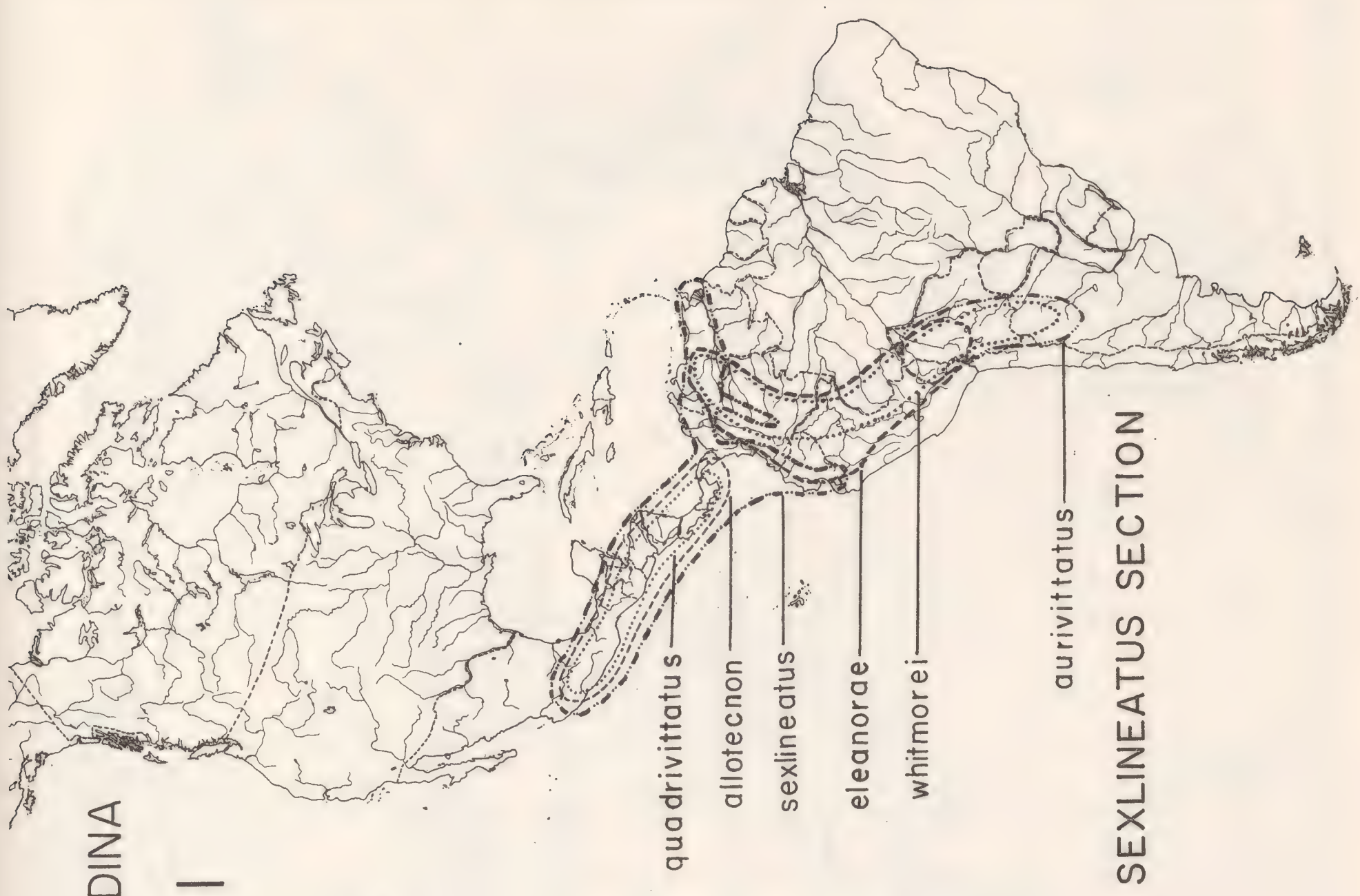
1905. Diptera, fam. Culicidae. In P. Wytsman, Genera Insectorum, Brussels, Desmet-Vertemeuil. Fasc. 26. 50 p.

1907. A monograph of the Culicidae or mosquitoes. v.4. London, Brit. Mus. (Natur. Hist.). 639 p.
1910. A monograph of the Culicidae or mosquitoes. v.5. London, Brit. Mus. (Natur. Hist.). 646 p.
- Theobald, F.V. and M. Grabham
1905. The mosquitoes or Culicidae of Jamaica. Kingston, Inst. Jamaica. 40 p.
- Thompson, G.A.
1947. A list of the mosquitoes of Jamaica, British West Indies. Mosquito News 7: 78-80.
1956. *Aedes stenei*, a new species of mosquito from Jamaica, B.W.I., with redescription of a closely related species (Diptera, Culicidae). Mosquito News 16: 196-200.
- Trapido, H. and P. Galindo
1957. Mosquitoes associated with sylvan yellow fever near Almirante, Panama. Amer. J. Trop. Med. Hyg. 6:114-144.
- Trapido, H., P. Galindo and S.J. Carpenter
1955. A survey of forest mosquitoes in relation to sylvan yellow fever in Panama Isthmian area. Amer. J. Trop. Med. Hyg. 4:525-542.
- Urich, F.W.
1913. Mosquitoes of Trinidad. Agr. Soc. Trinidad Tobago, Proc. 13:525-530 (Pap. 574).
- Vargas, L.
1956. Especies y distribucion de mosquitos mexicanos no Anofelinos (Insecta, Diptera). Inst. Salub. Enferm. Trop., Rev. 16:19-36.
- Whitman, L.
1951. The Arthropod vectors of yellow fever. In G.K. Strode (ed.). Yellow Fever. New York, Mc Graw Hill. 710 p.
- Whitman, L. and P.C.A. Antunes
1937. Studies on the capacity of various Brazilian mosquitoes, representing the genera *Psorophora*, *Aedes*, *Mansonia* and *Culex* to transmit yellow fever. Amer. J. Trop. Med. 17:803-823.

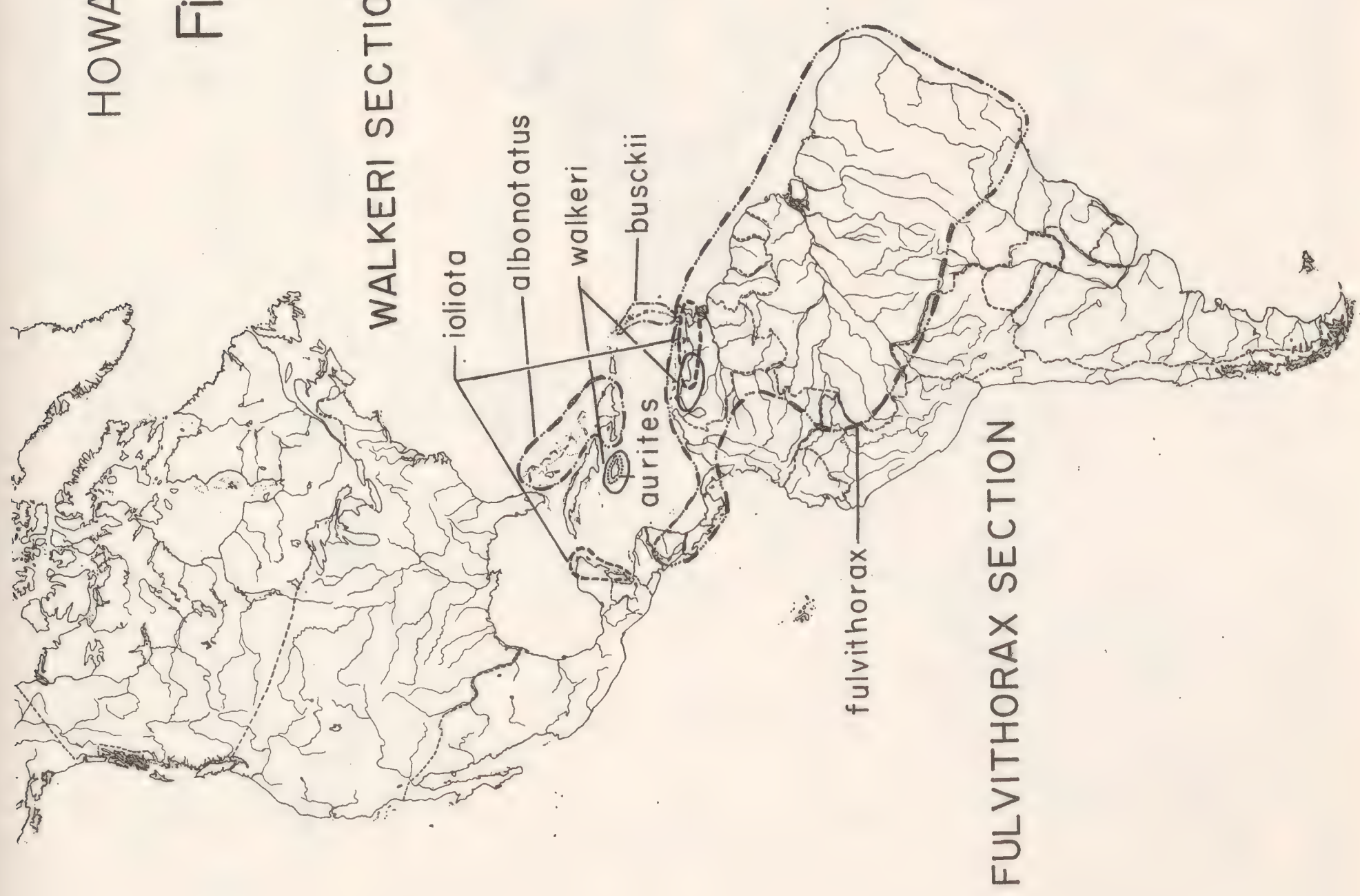
FIGURES

1. Distribution of the groups of *Howardina*
2. Distribution of the species of the Fulvithorax Section
3. Distribution of the species of the Walkeri Section
4. Distribution of *Aedes (H.) sexlineatus*
5. Distribution of the species of the Quadrivittatus, Whitmorei and Aurivittatus Groups
6. Distribution of the species of the Allotecnion and Eleanorae Groups
7. Biting-landing cycle of *Howardina* species near Porus, Jamaica
8. Mesonotal scale pattern of *Howardina* species
9. Mesonotal scale pattern of *Howardina* species
10. *Aedes (H.) fulvithorax*; pleuron, male genitalia and pupa
11. *Aedes (H.) fulvithorax*; larva
12. *Aedes (H.) septemstriatus*; male genitalia and pupa
13. *Aedes (H.) septemstriatus*; larva
14. *Aedes (H.) arborealis*; male genitalia and pupa
15. *Aedes (H.) arborealis*; larva
16. *Aedes (H.) walkeri*; adult morphology
17. *Aedes (H.) walkeri*; pleuron, male genitalia and pupa
18. *Aedes (H.) walkeri*; larva
19. *Aedes (H.) aurites*; male genitalia and pupa
20. *Aedes (H.) aurites*; larva
21. *Aedes (H.) grabhami*; male genitalia and pupa
22. *Aedes (H.) grabhami*; larva
23. *Aedes (H.) inaequalis*; male genitalia and pupa
24. *Aedes (H.) inaequalis*; larva
25. *Aedes (H.) stenei*; male genitalia and pupa
26. *Aedes (H.) stenei*; larva
27. *Aedes (H.) ioliota*; male genitalia and pupa
28. *Aedes (H.) ioliota*; larva
29. *Aedes (H.) cozumelensis*; male genitalia and pupa
30. *Aedes (H.) cozumelensis*; larva
31. *Aedes (H.) albonotatus*; male genitalia and pupa
32. *Aedes (H.) bahamensis*; male genitalia and pupa
33. *Aedes (H.) bahamensis*; larva
34. *Aedes (H.) busckii*; male genitalia and pupa
35. *Aedes (H.) busckii*; larva
36. *Aedes (H.) quadrivittatus*; pleuron, male genitalia and pupa
37. *Aedes (H.) quadrivittatus*; larva
38. *Aedes (H.) lorraineae*; larva
39. *Aedes (H.) brevis*; male genitalia and pupa
40. *Aedes (H.) brevis*; larva
41. *Aedes (H.) spinosus*; male genitalia and pupa
42. *Aedes (H.) spinosus*; larva
43. *Aedes (H.) sexlineatus*; male genitalia and pupa
44. *Aedes (H.) sexlineatus*; larva
45. *Aedes (H.) whitmorei*; male genitalia and pupa
46. *Aedes (H.) whitmorei*; larva
47. *Aedes (H.) allotecnion*; male genitalia and pupa

48. *Aedes* (H.) *allotecnnon*; larva
49. *Aedes* (H.) *guerrero*; larva
50. *Aedes* (H.) *eleanorae*; male genitalia and pupa
51. *Aedes* (H.) *eleanorae*; larva
52. *Aedes* (H.) *marinkellei*; pupa
53. *Aedes* (H.) *marinkellei*; larva
54. *Aedes* (H.) *leei*; male genitalia and pupa
55. *Aedes* (H.) *leei*; larva
56. *Aedes* (H.) *osornoi*; male genitalia and pupa
57. *Aedes* (H.) *osornoi*; larva
58. *Aedes* (H.) *aureolineatus*, *pseudodominicii*, *ecuadoriensis* and *brevivittatus*; male genitalia



SEXLINEATUS SECTION

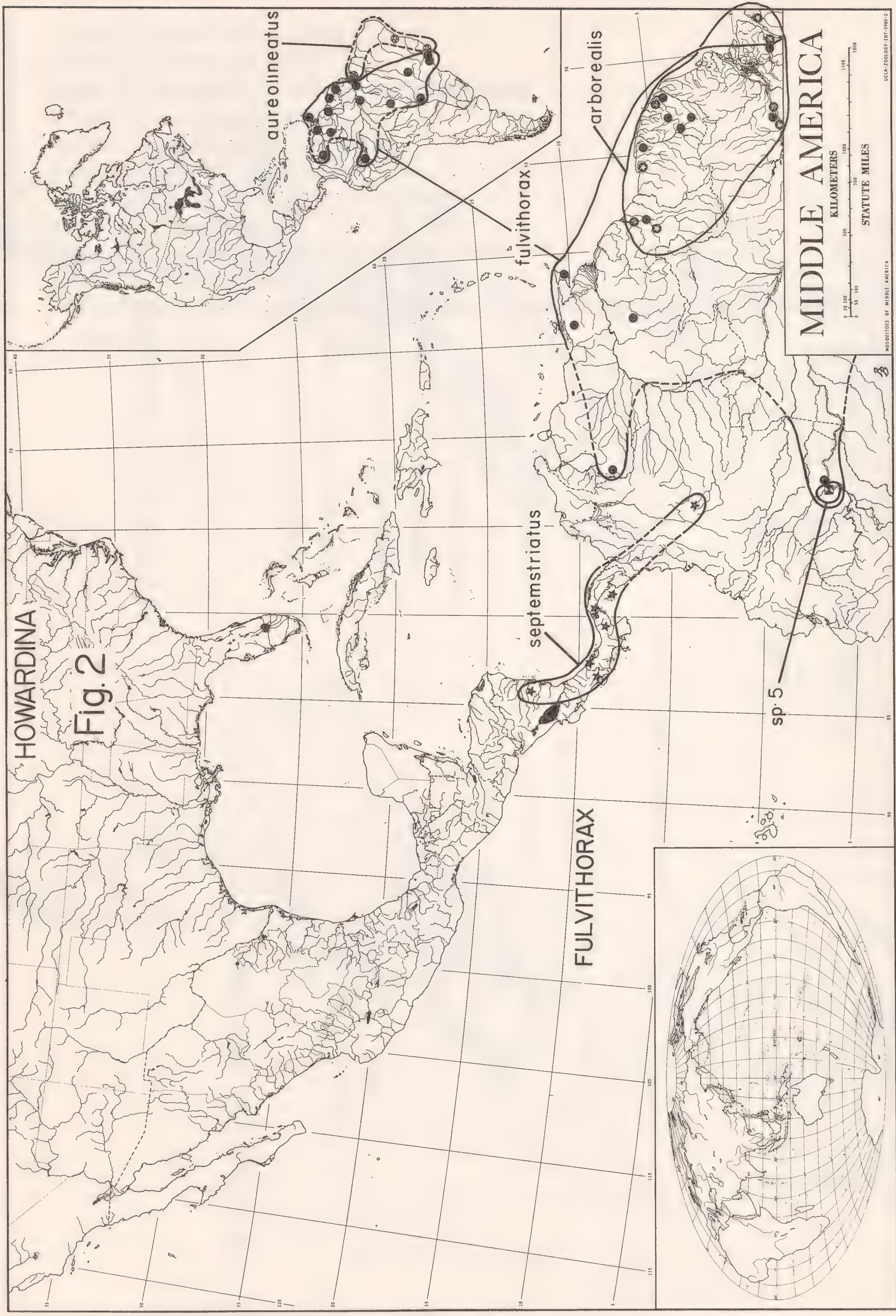


FULVITHORAX SECTION

HOWARDINA

Fig. I

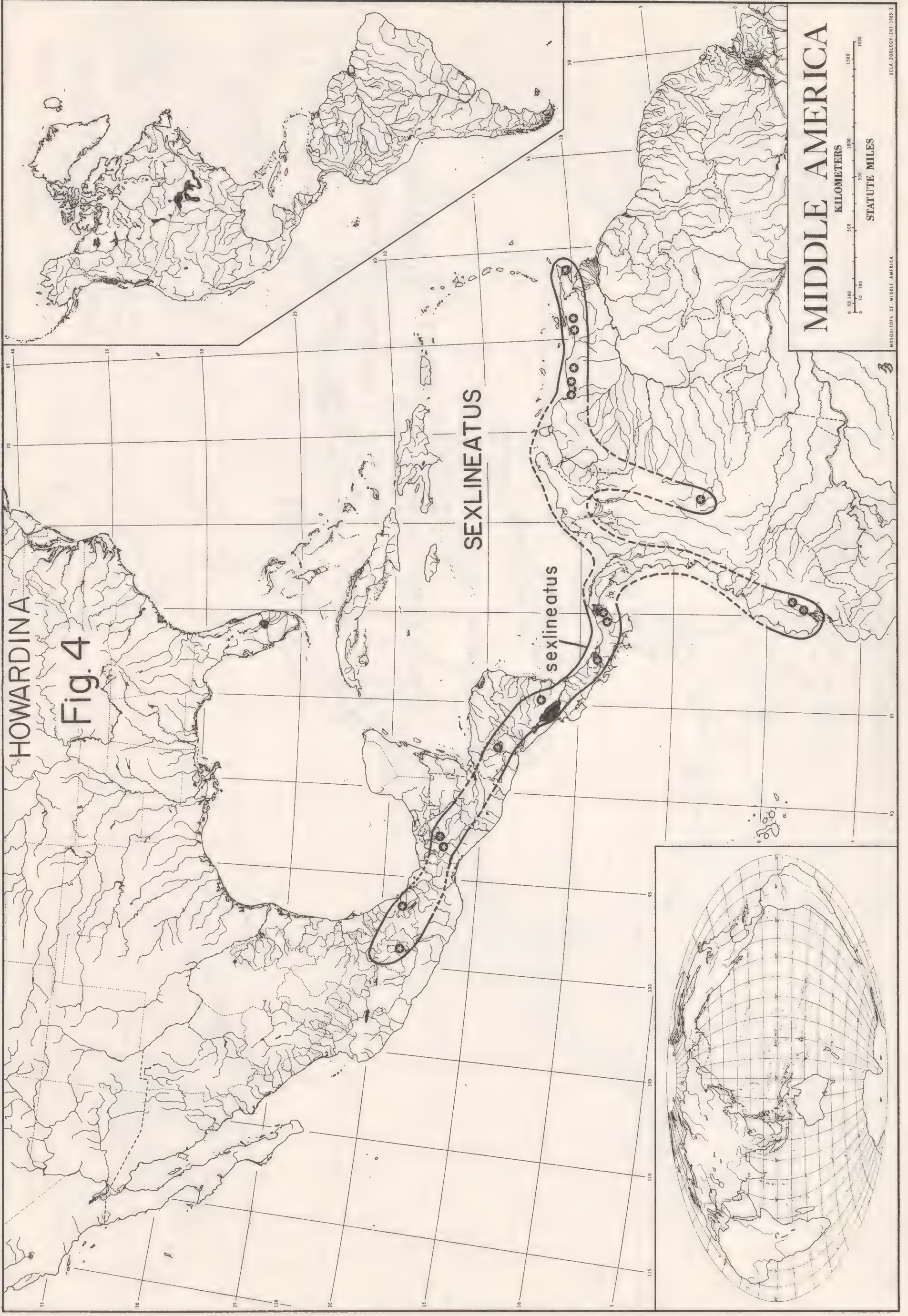
WALKERI SECTION

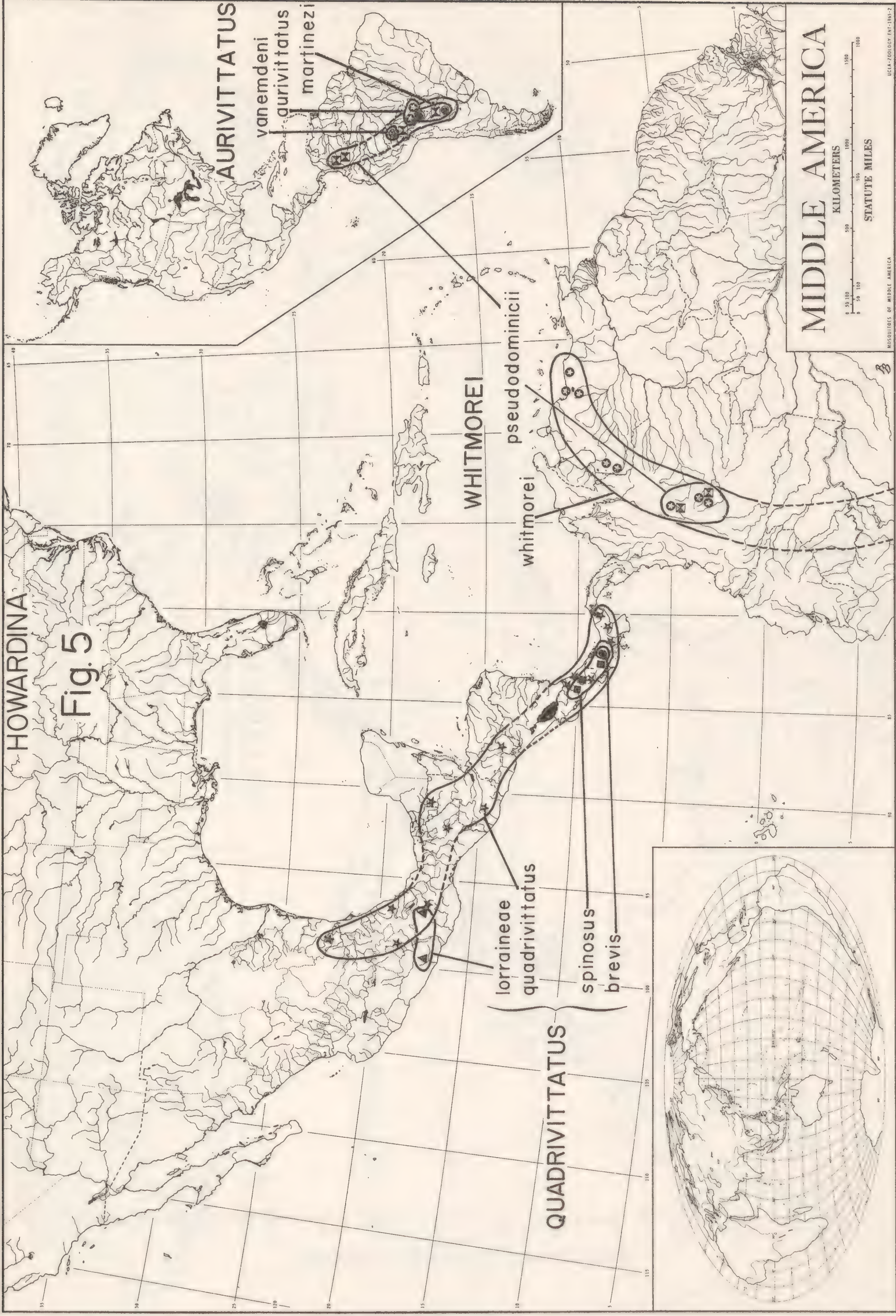


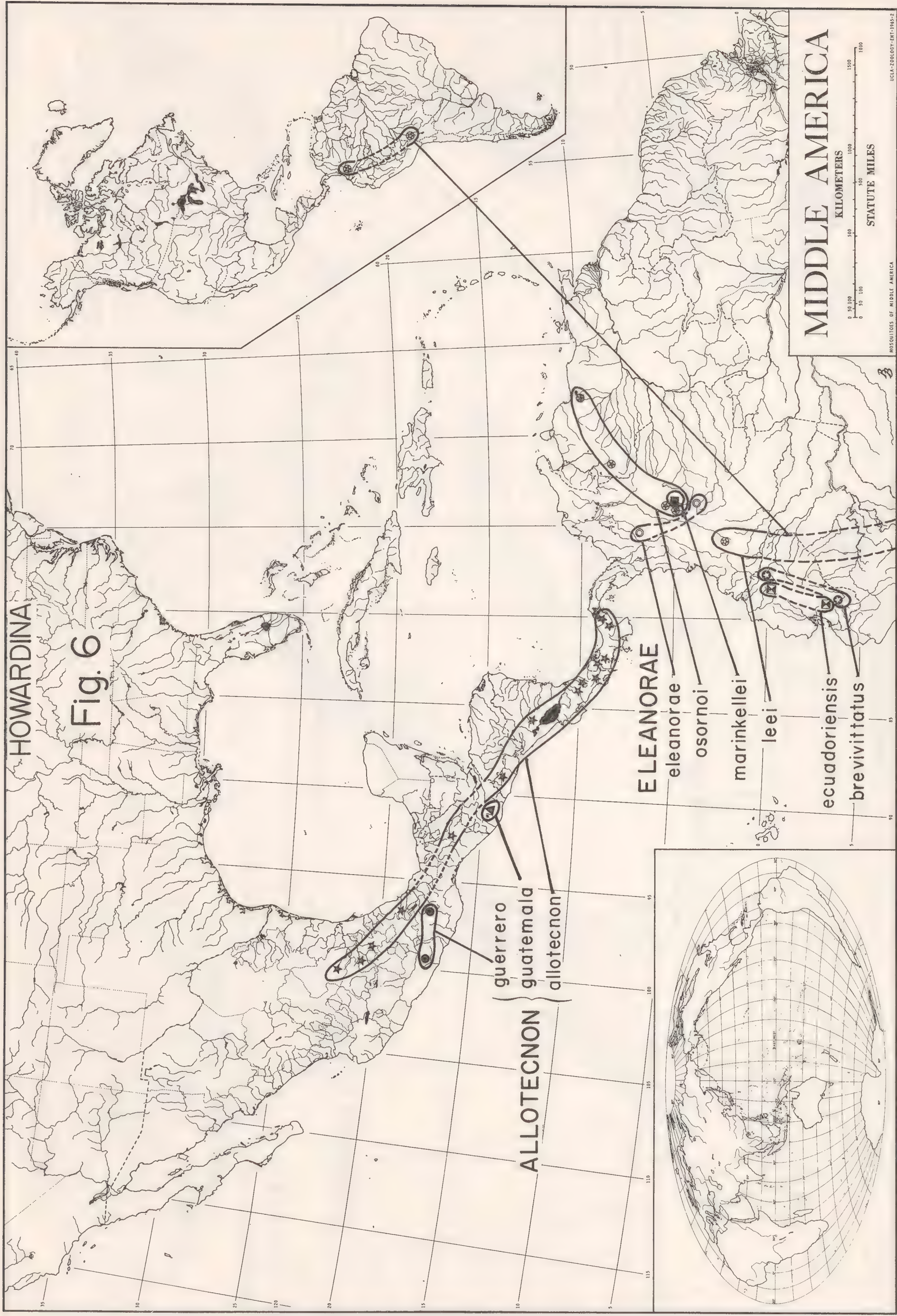
HOWARDINA

Fig. 3



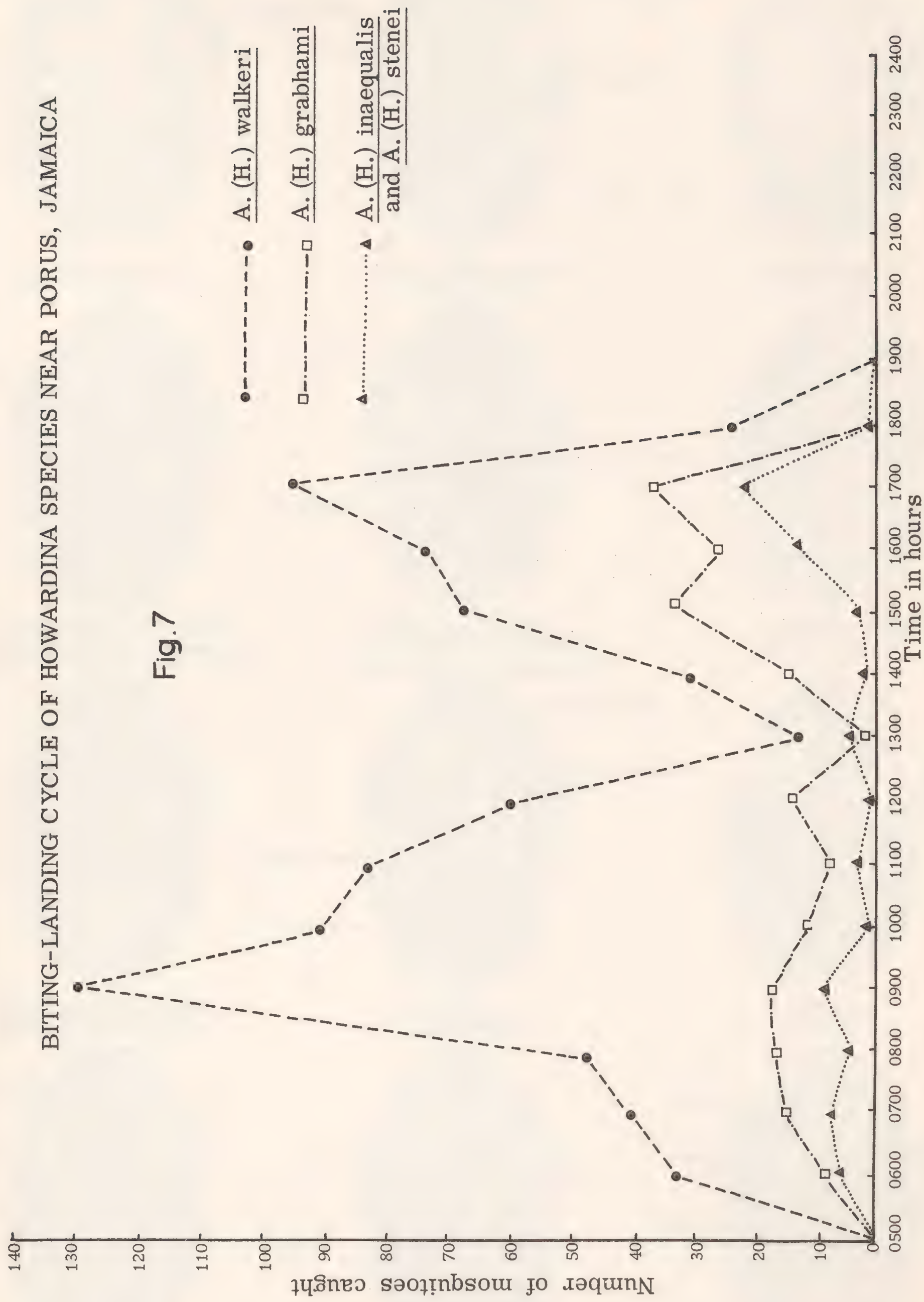






BITING-LANDING CYCLE OF HOWARDINA SPECIES NEAR PORUS, JAMAICA

Fig.7

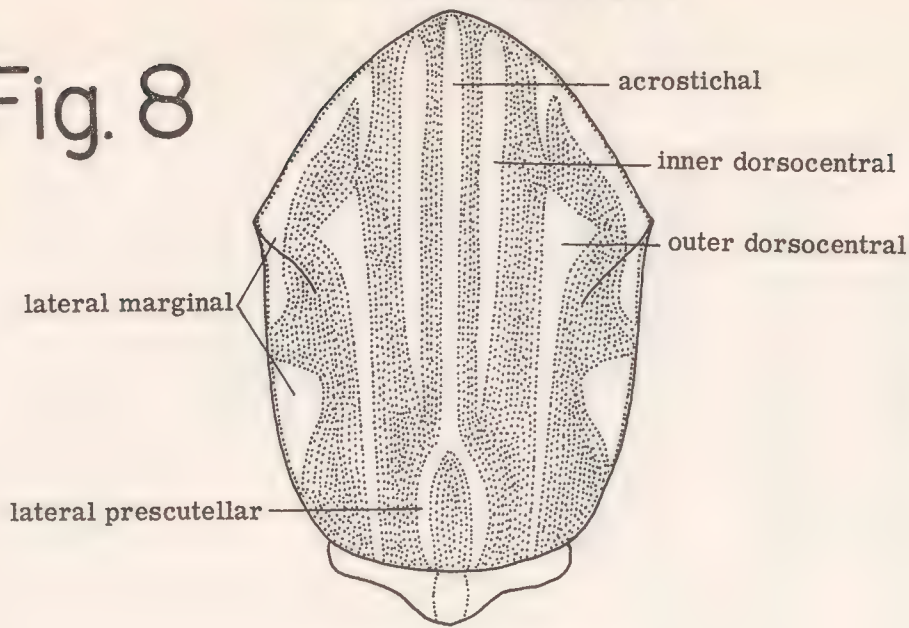


HOWARDINA

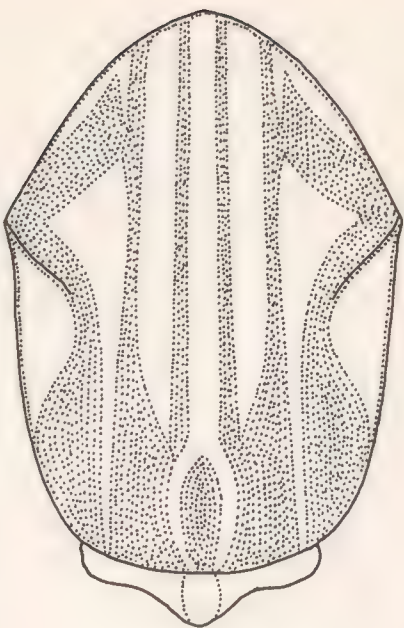
Fig. 8



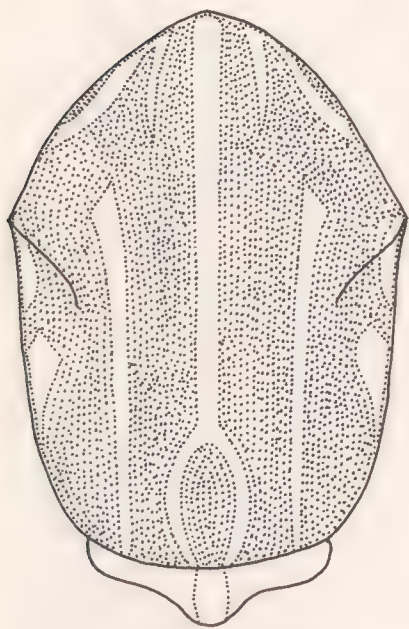
fulvithorax



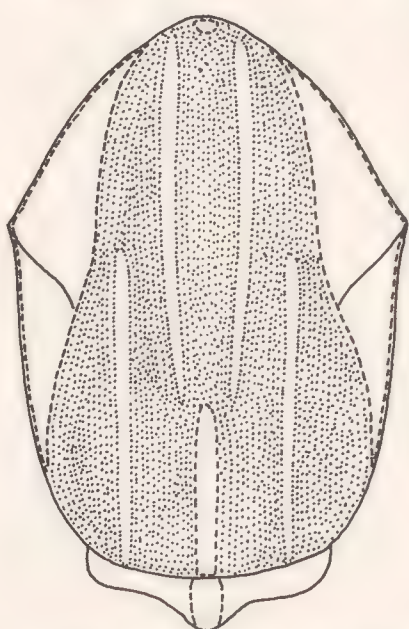
septemstriatus



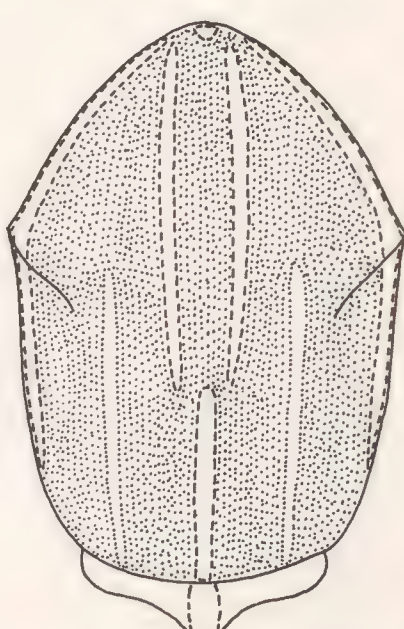
arborealis



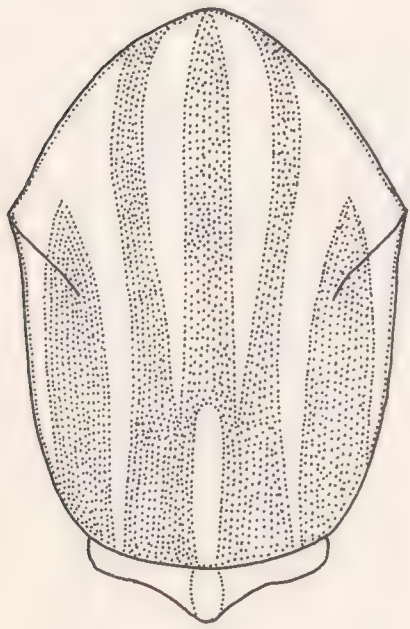
aureolineatus



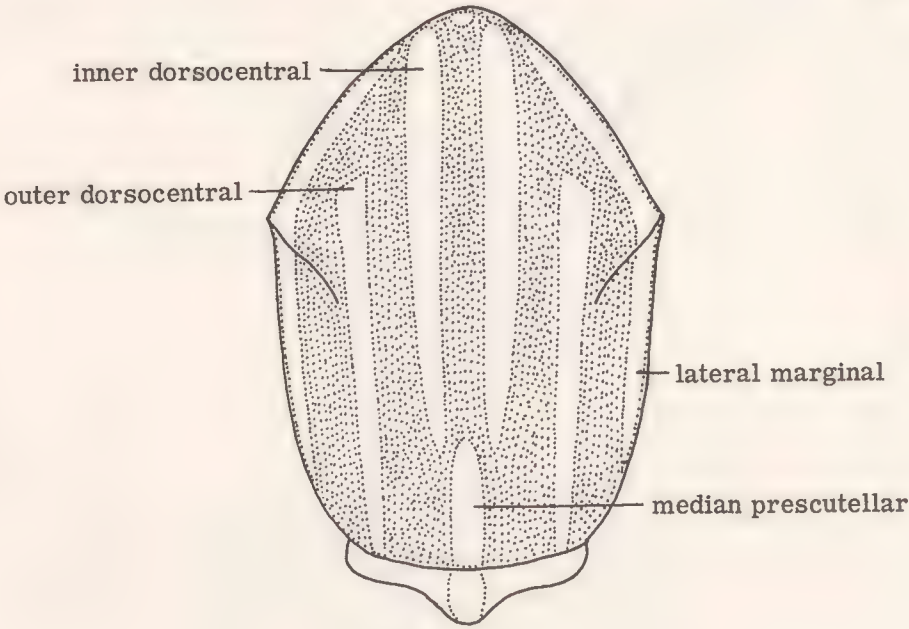
walkeri, argyrites



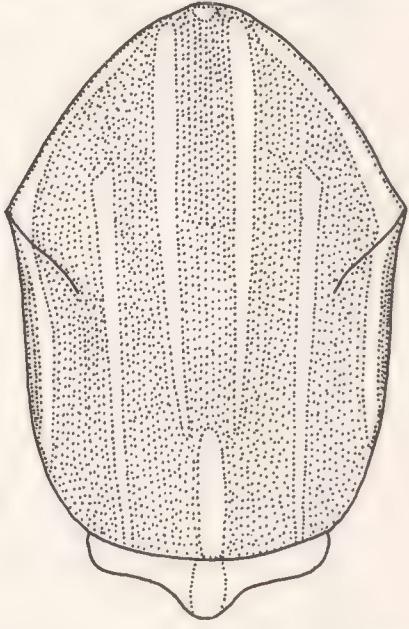
ioliota, cozumelensis,
albonotatus, bahamensis,



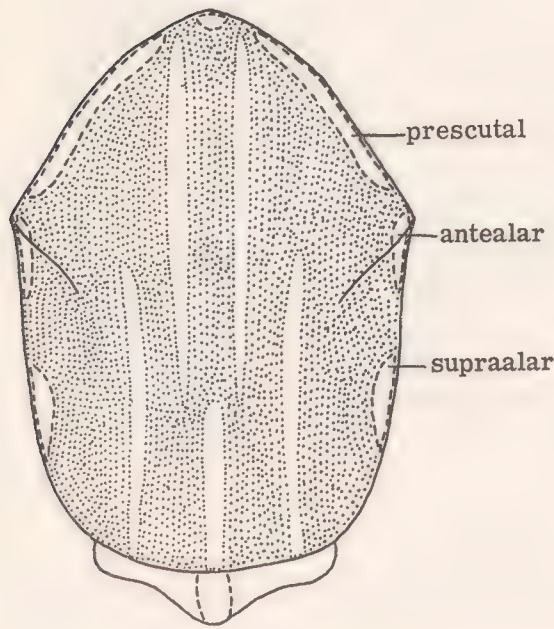
aurites



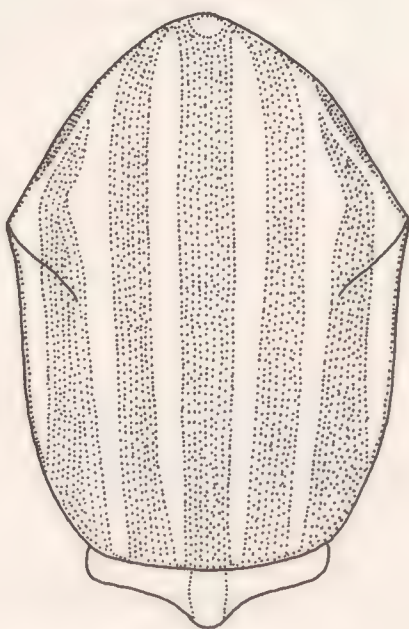
grabhami



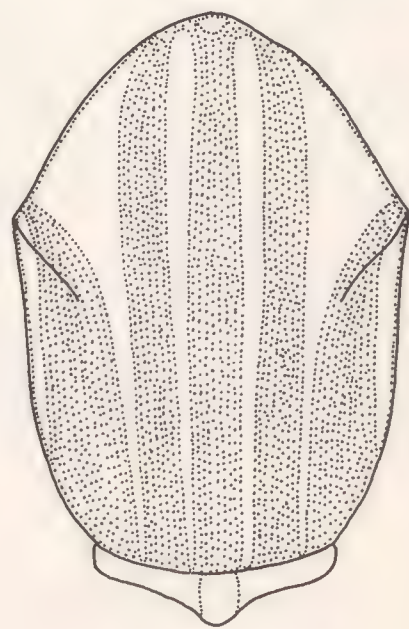
stenei, inaequalis



busckii



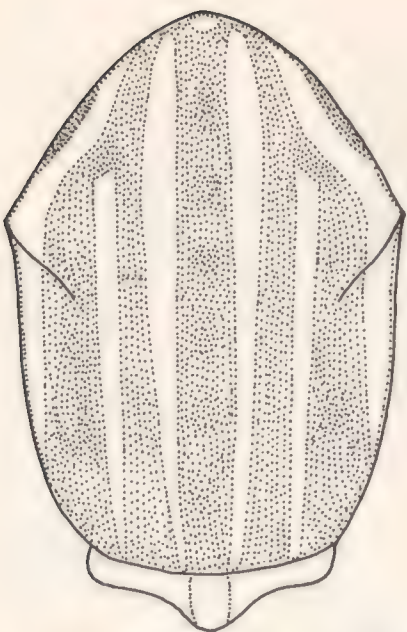
quadrivittatus



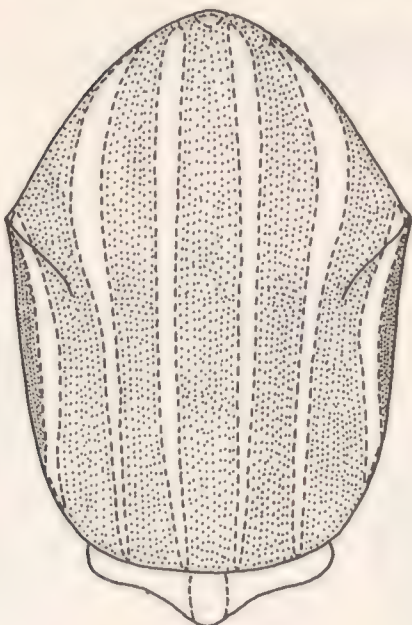
lorraineae

HOWARDINA

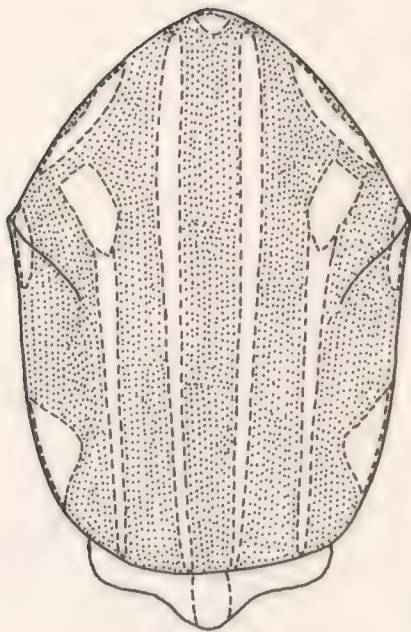
Fig. 9



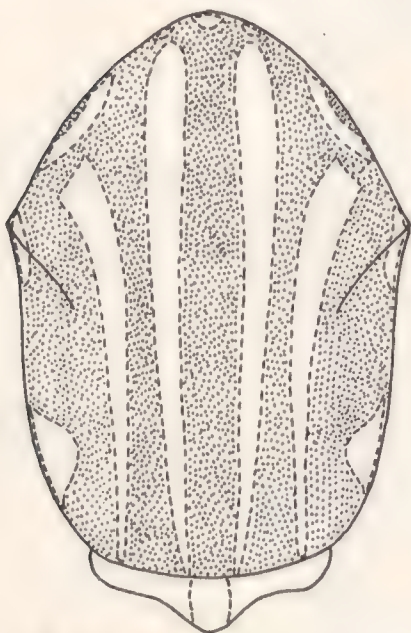
brevis, spinosus



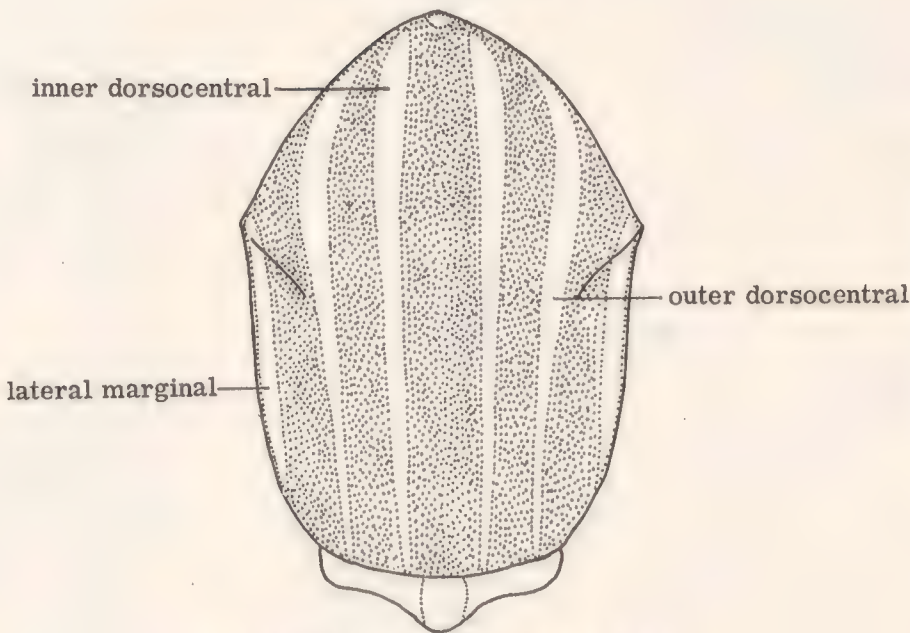
sexlineatus



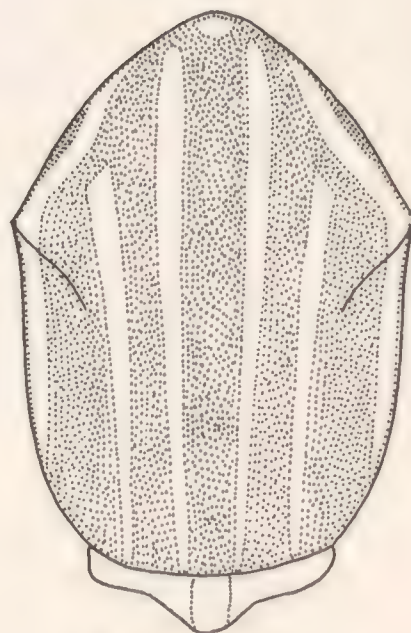
whitmorei



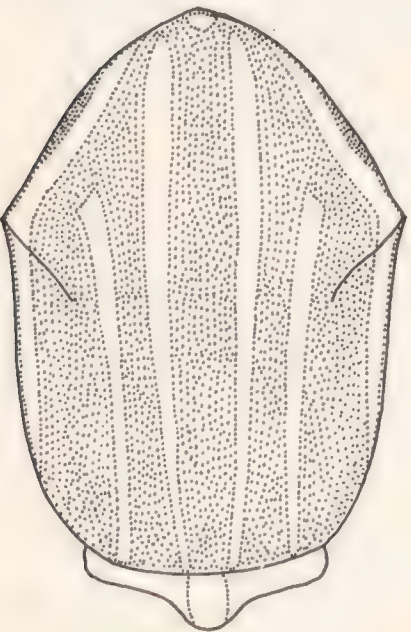
pseudodominicii



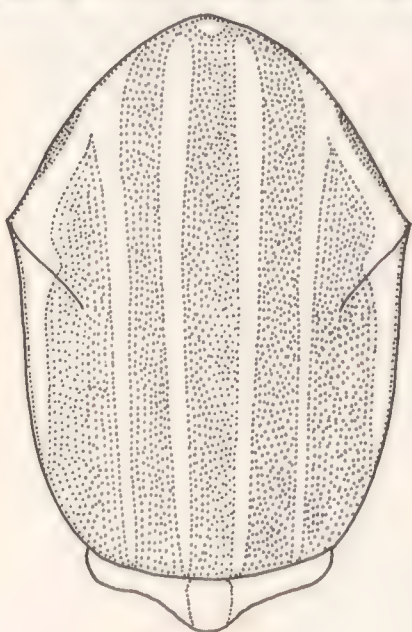
allotecnnon, guerrero,
guatemala, vanemdeni



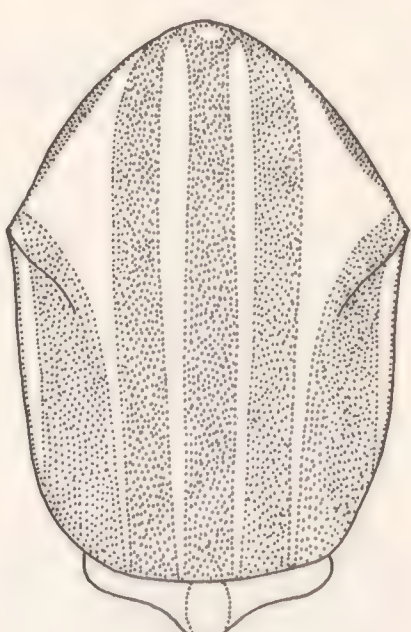
eleanorae



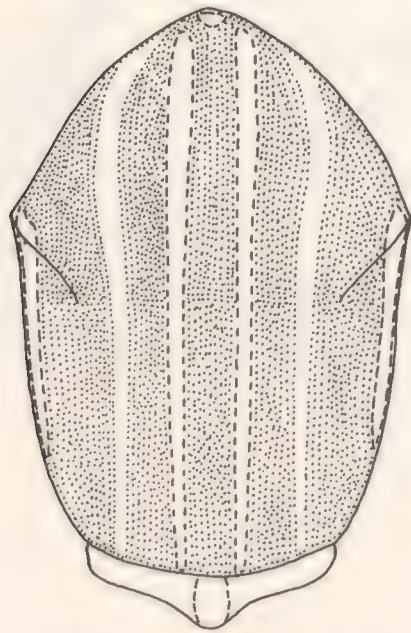
leei, brevivittatus



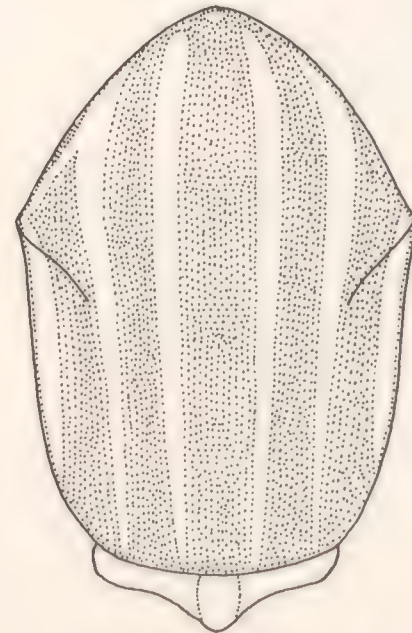
marinkellei



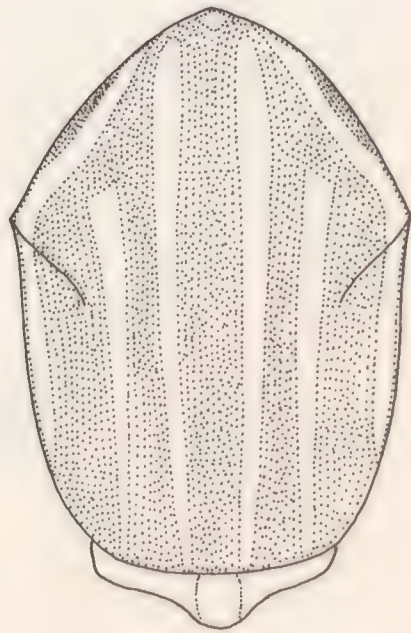
osornoi



ecuadoriensis



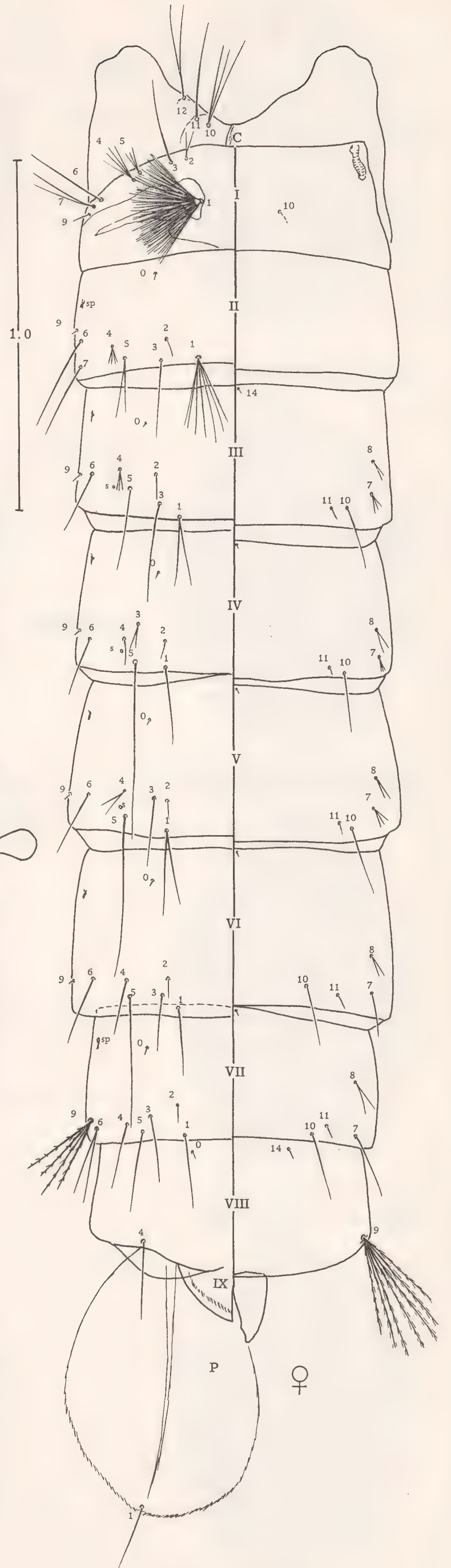
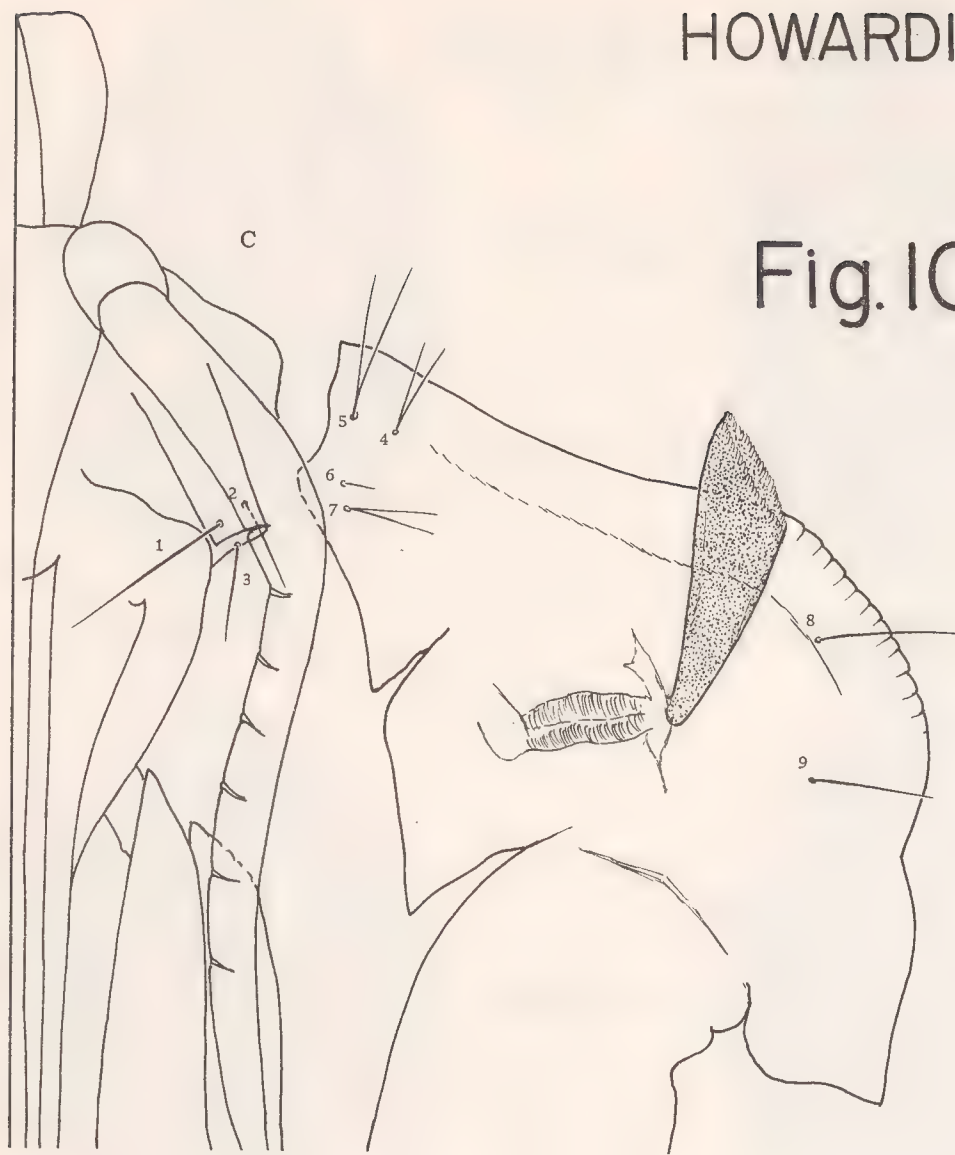
aurivittatus



martinezi

HOWARDINA

Fig. 10



fulvithorax

TR 591-121
Monos Island
Trinidad

HOWARDINA

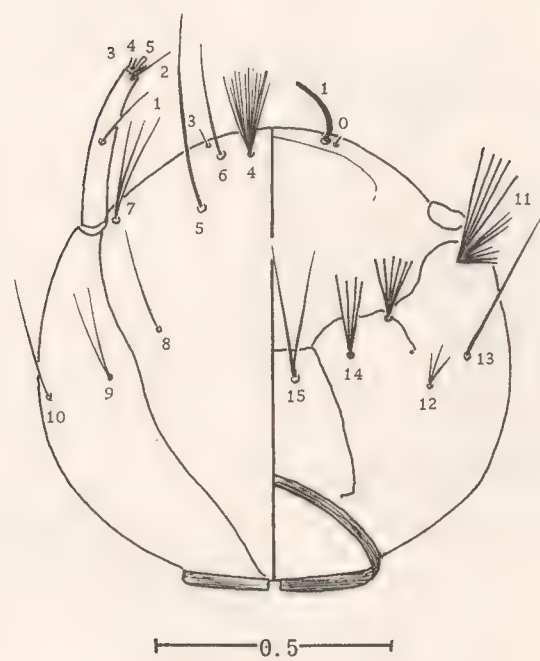
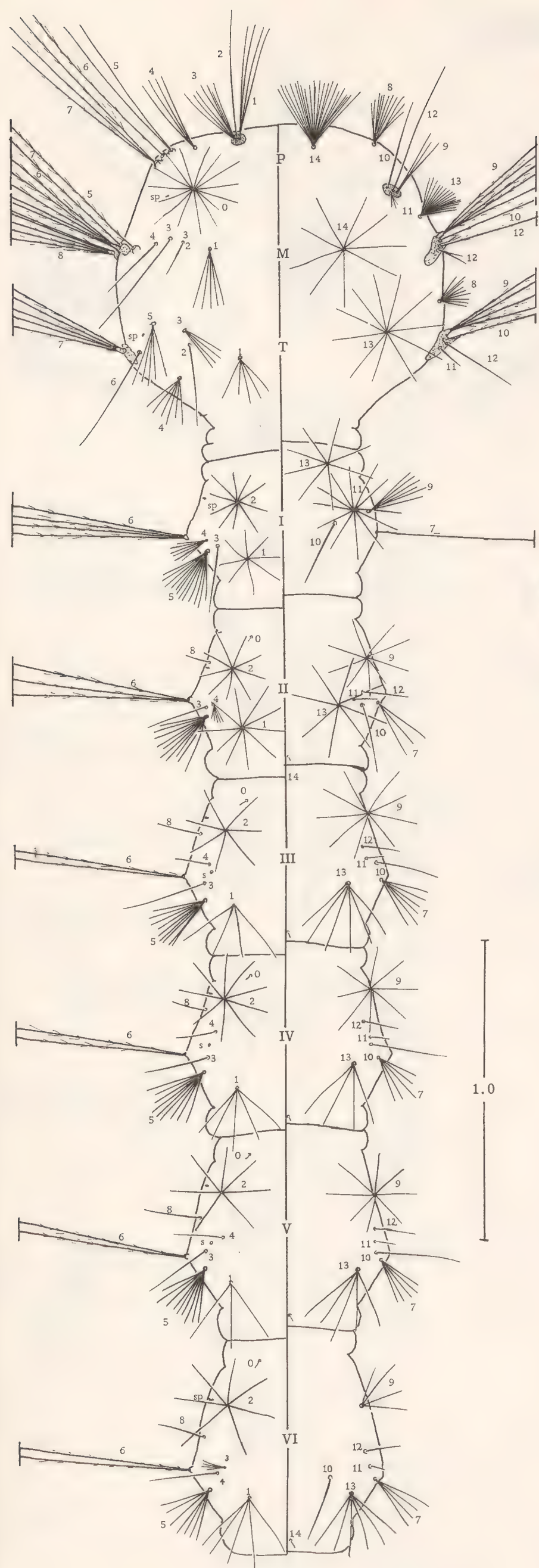
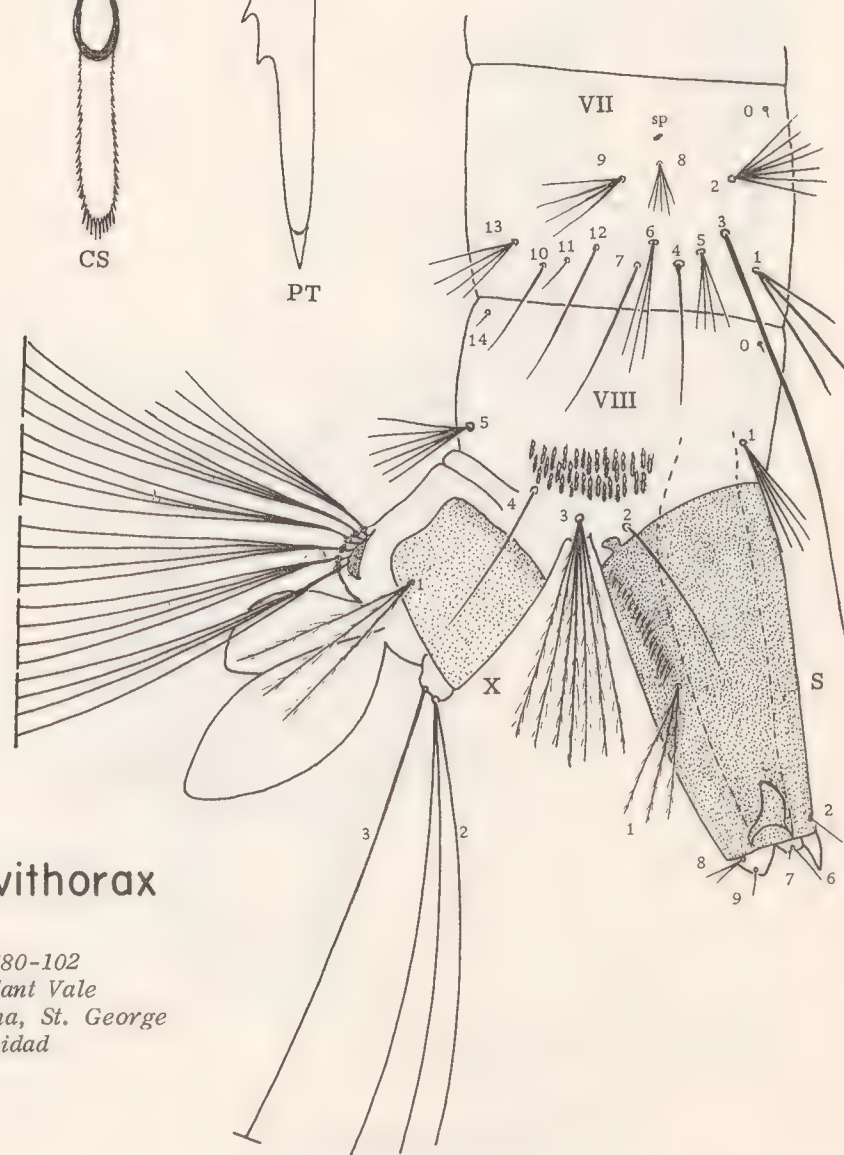
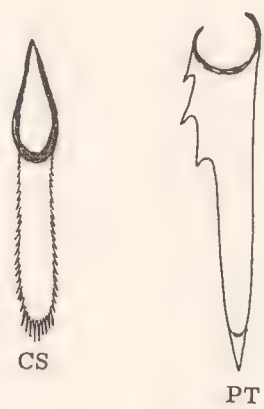
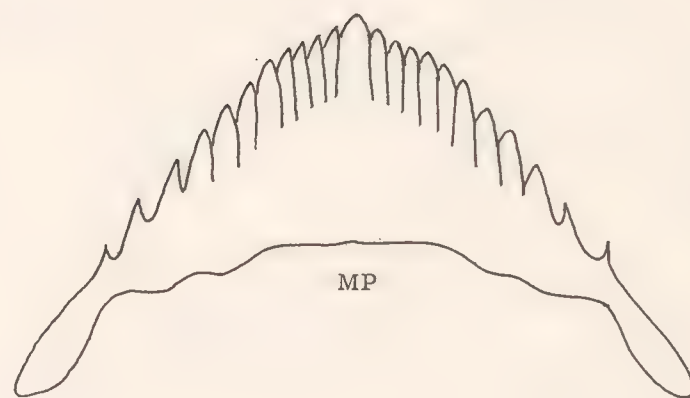


Fig. II

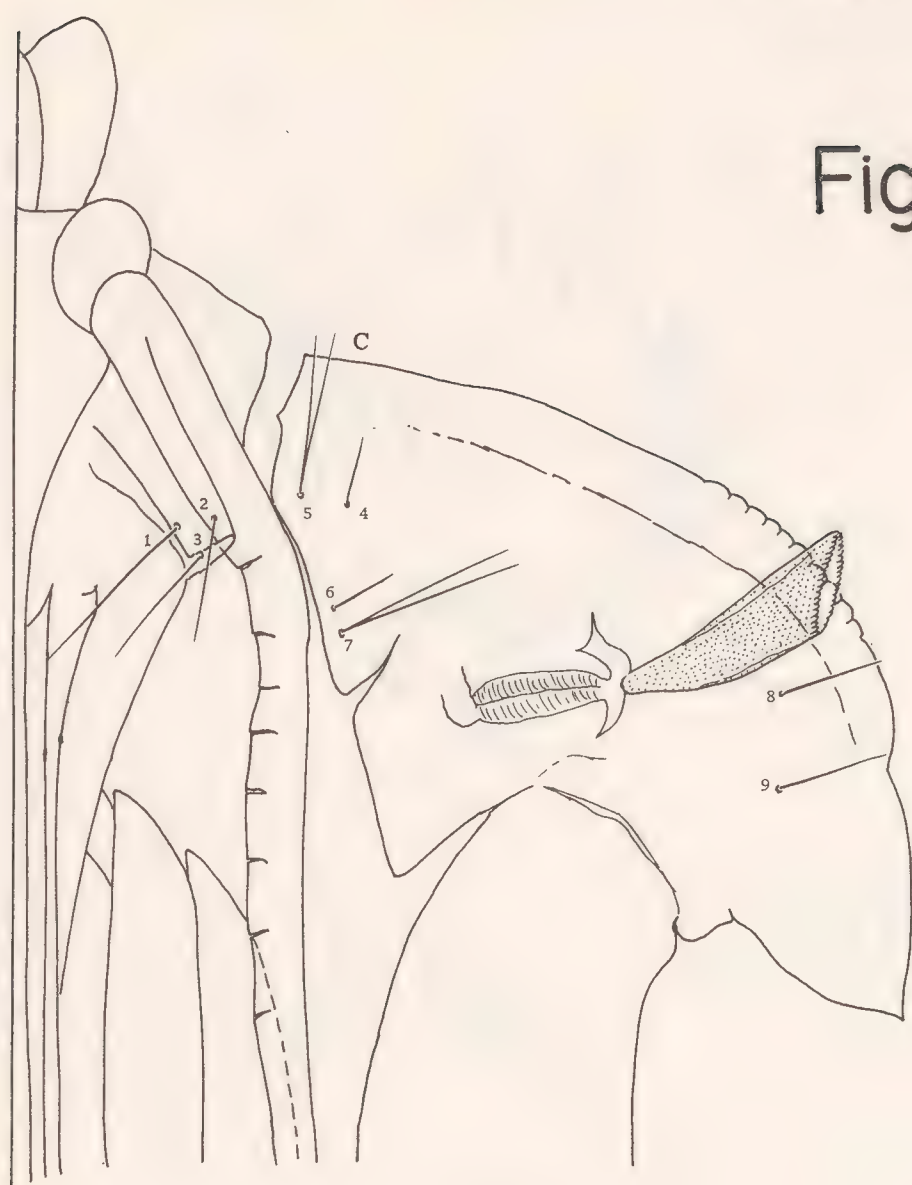


fulvithorax

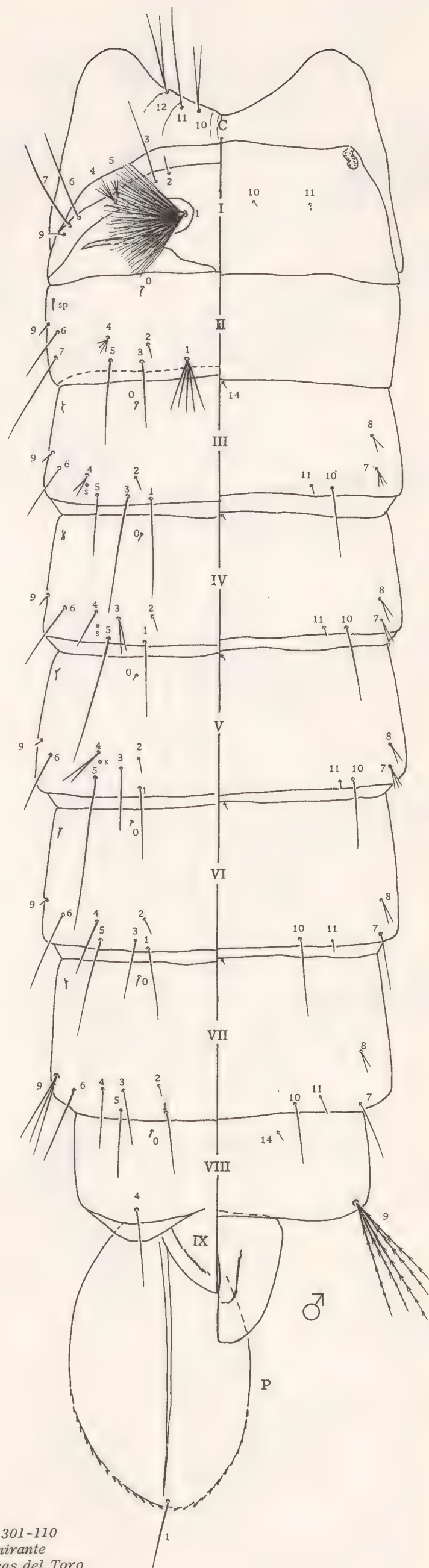
TR 680-102
Verdant Vale
Arima, St. George
Trinidad

HOWARDINA

Fig. 12



septemstriatus



PA 301-110
Almirante
Bocas del Toro
Panama

HOWARDINA

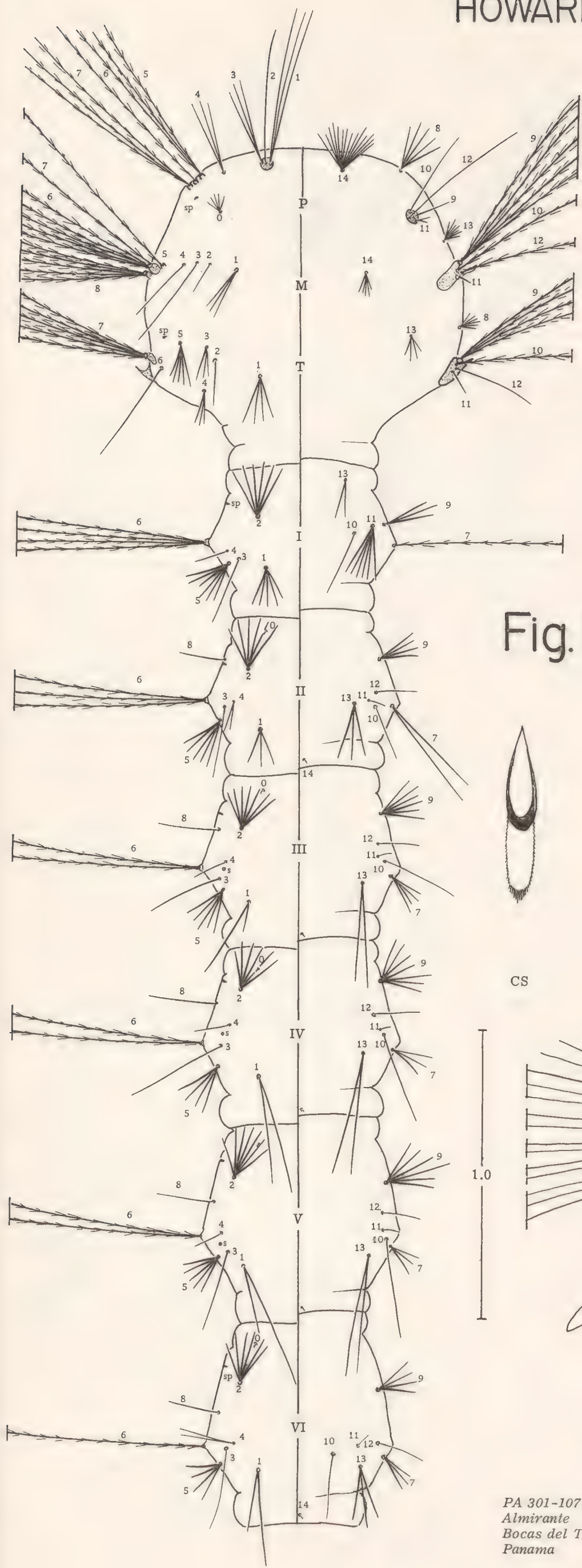
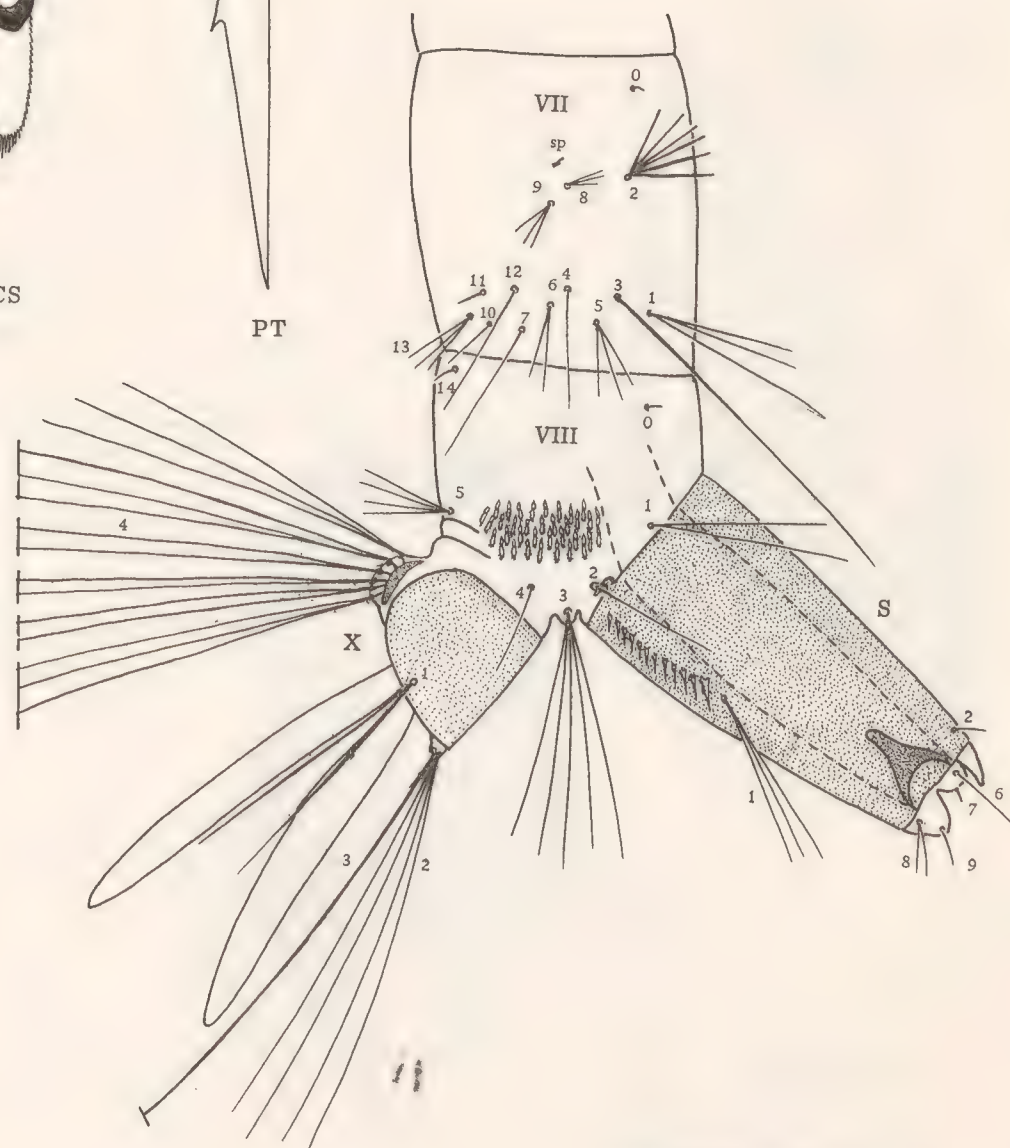
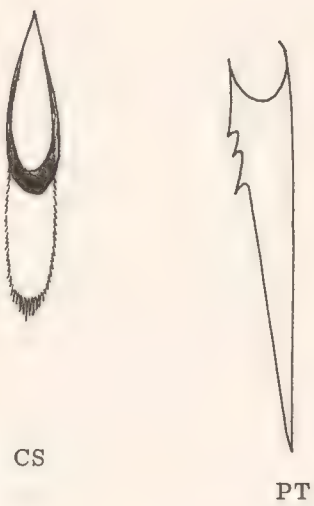
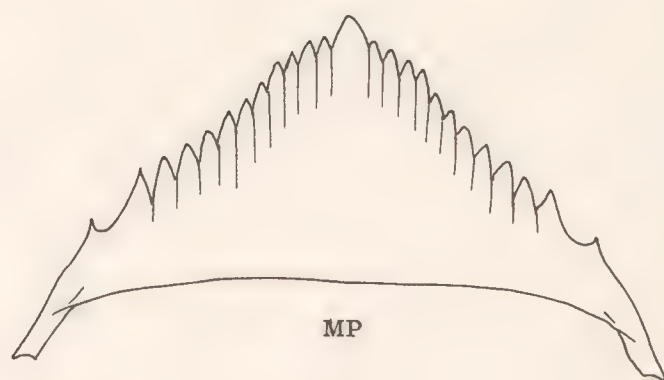
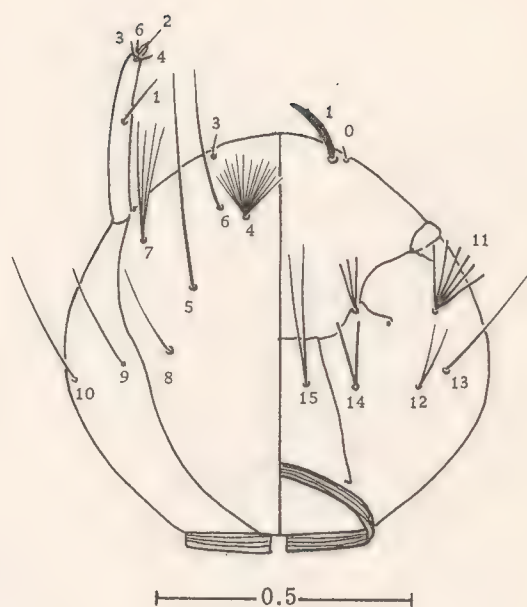


Fig. 13

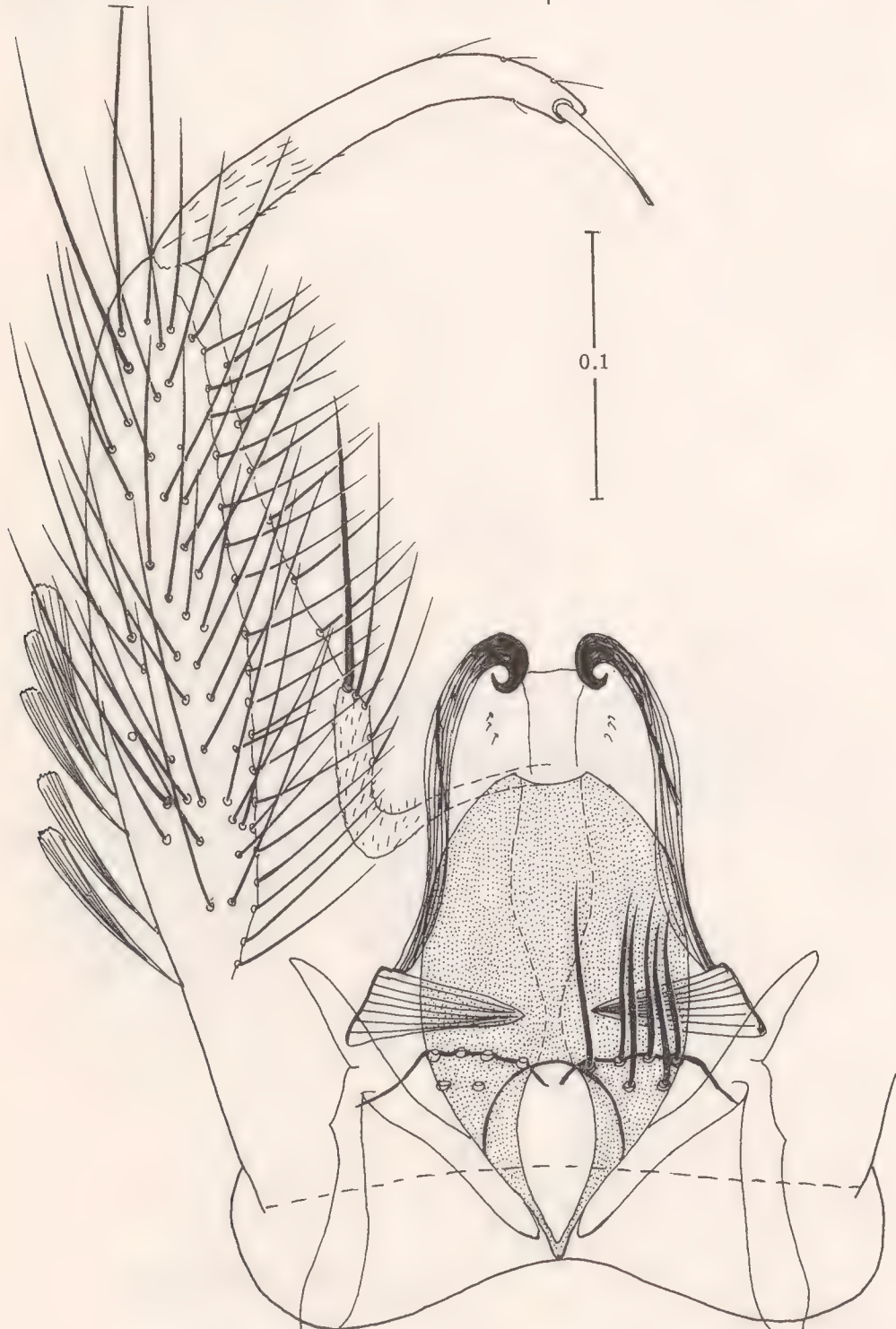
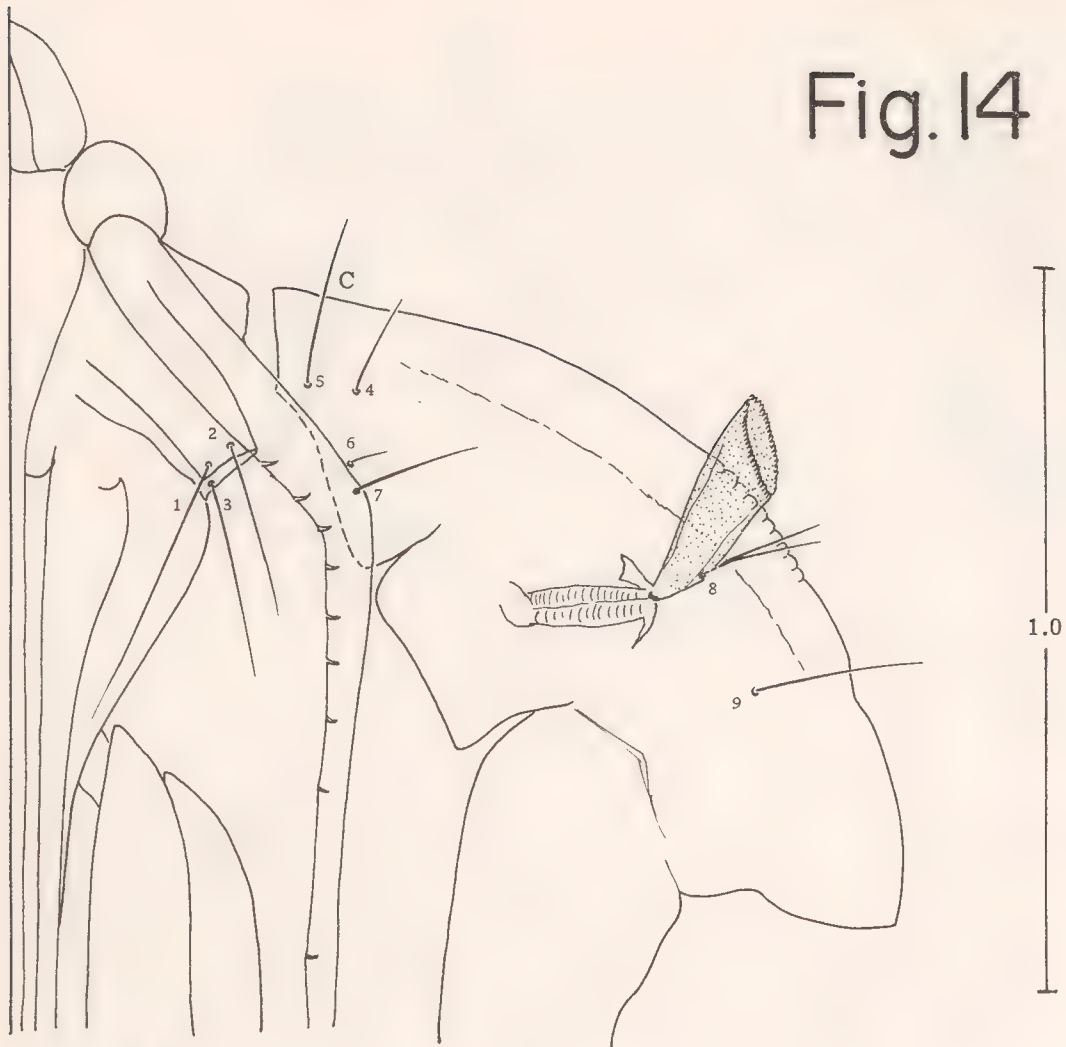


septemstriatus

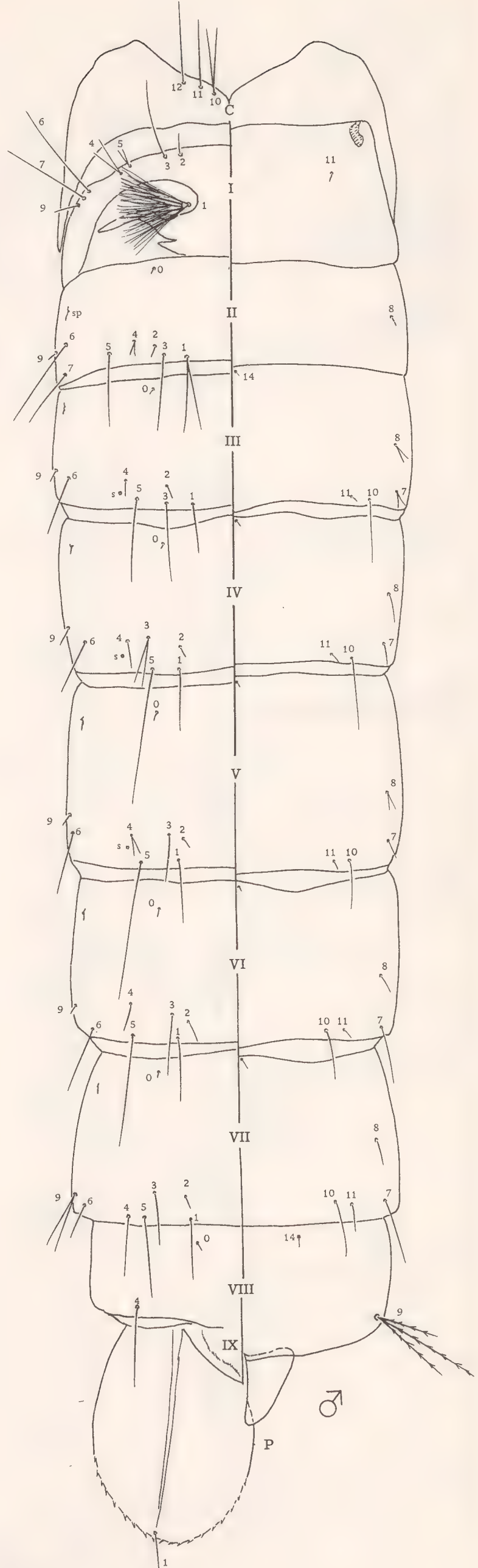
PA 301-107
Almirante
Bocas del Toro
Panama

HOWARDINA

Fig. 14



arborealis



Surinam

HOWARDINA

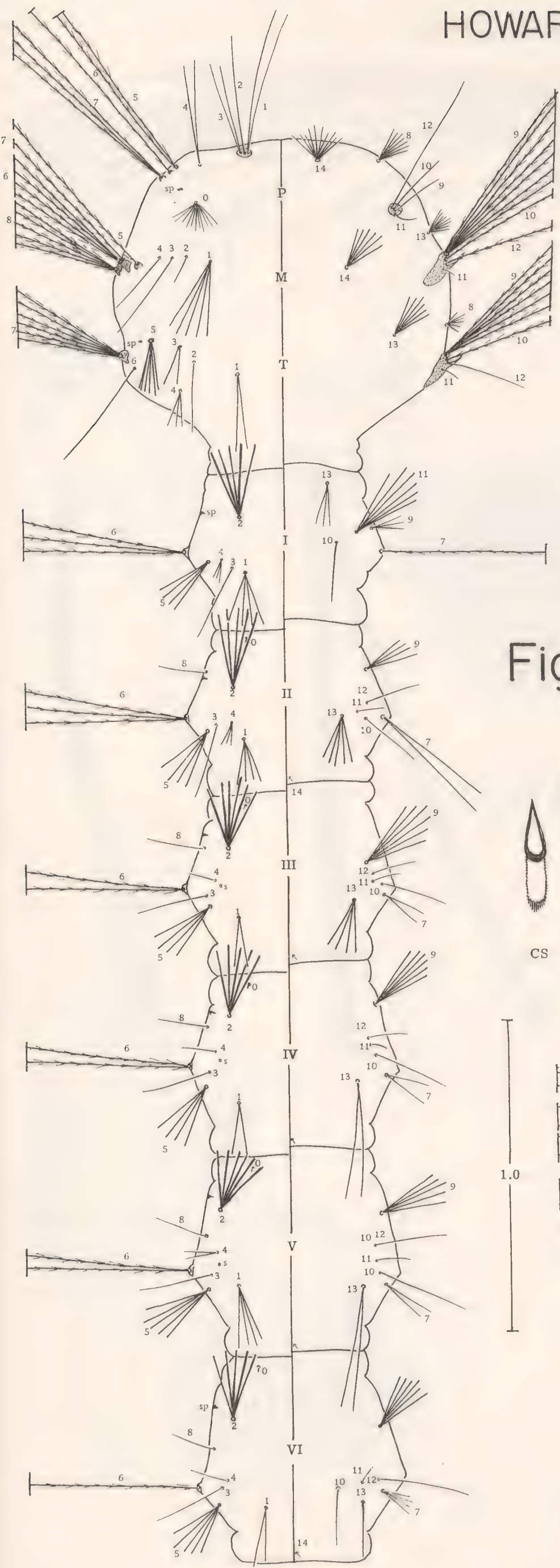
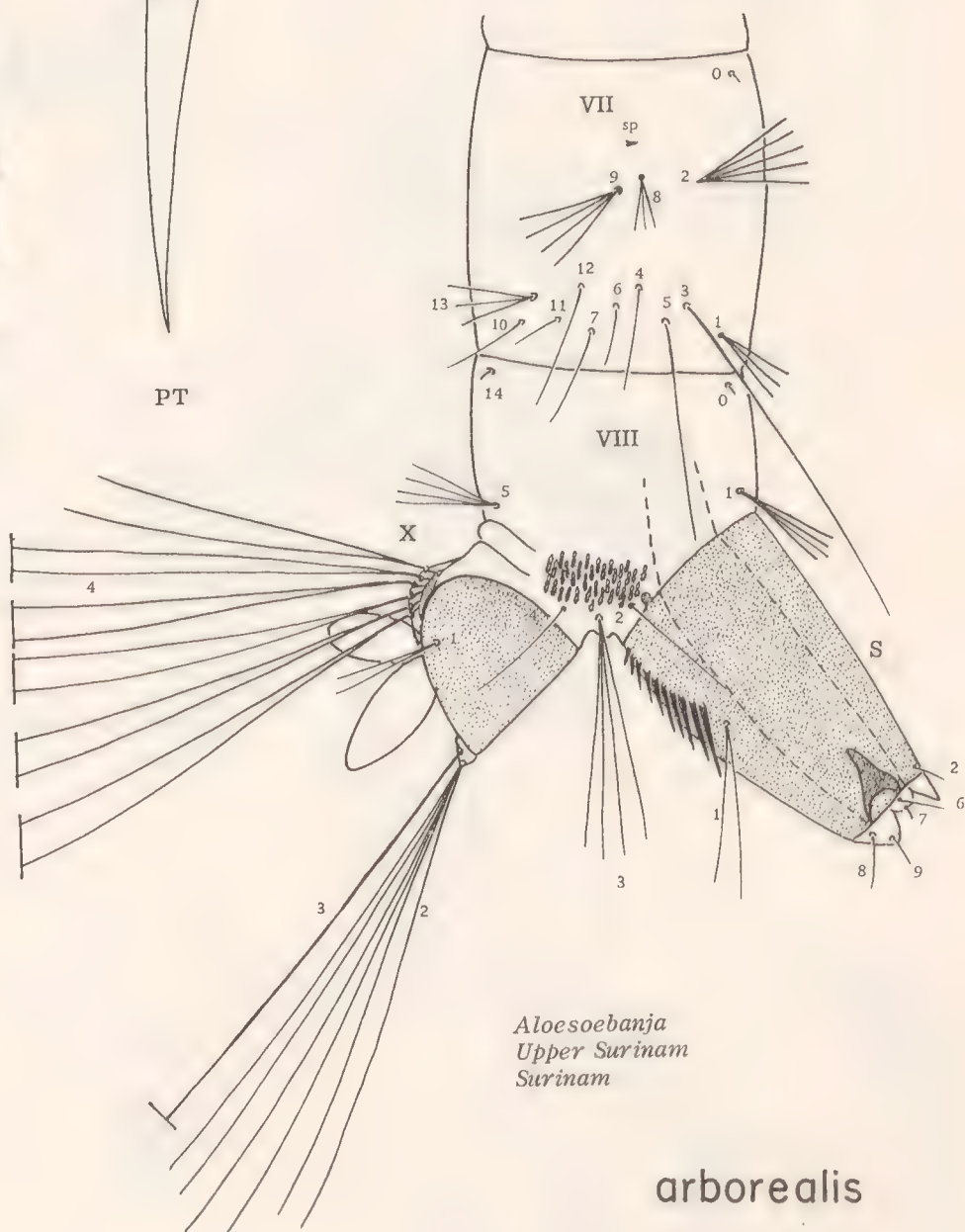
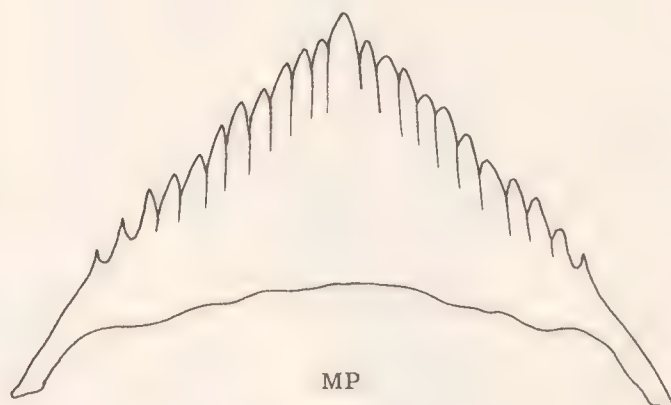
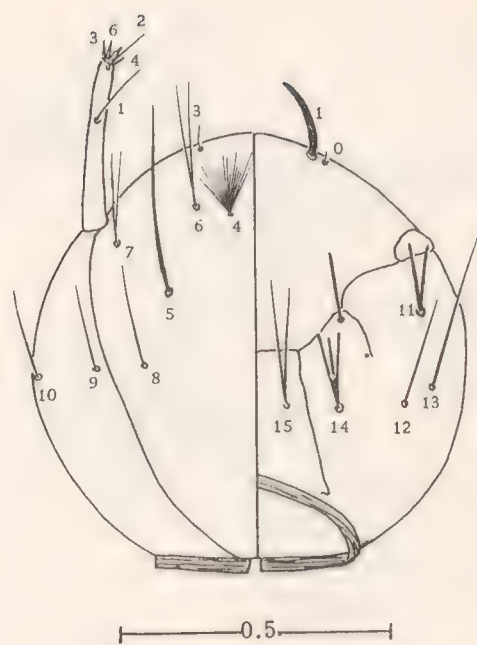
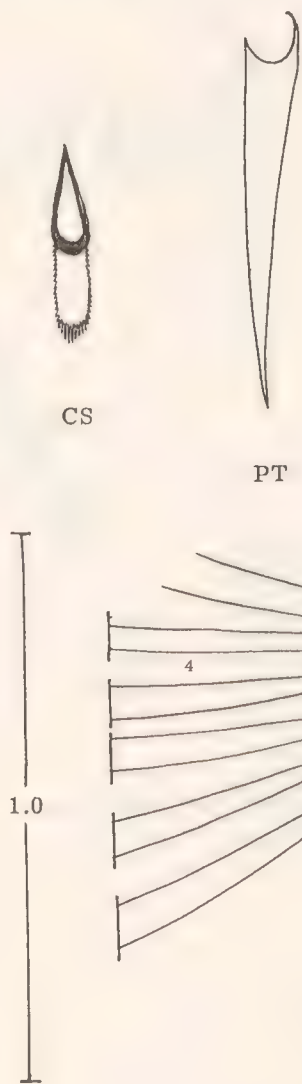


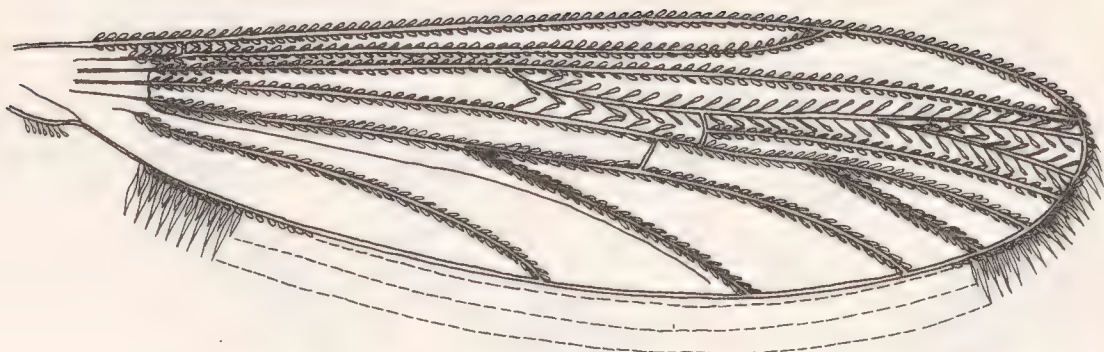
Fig. 15



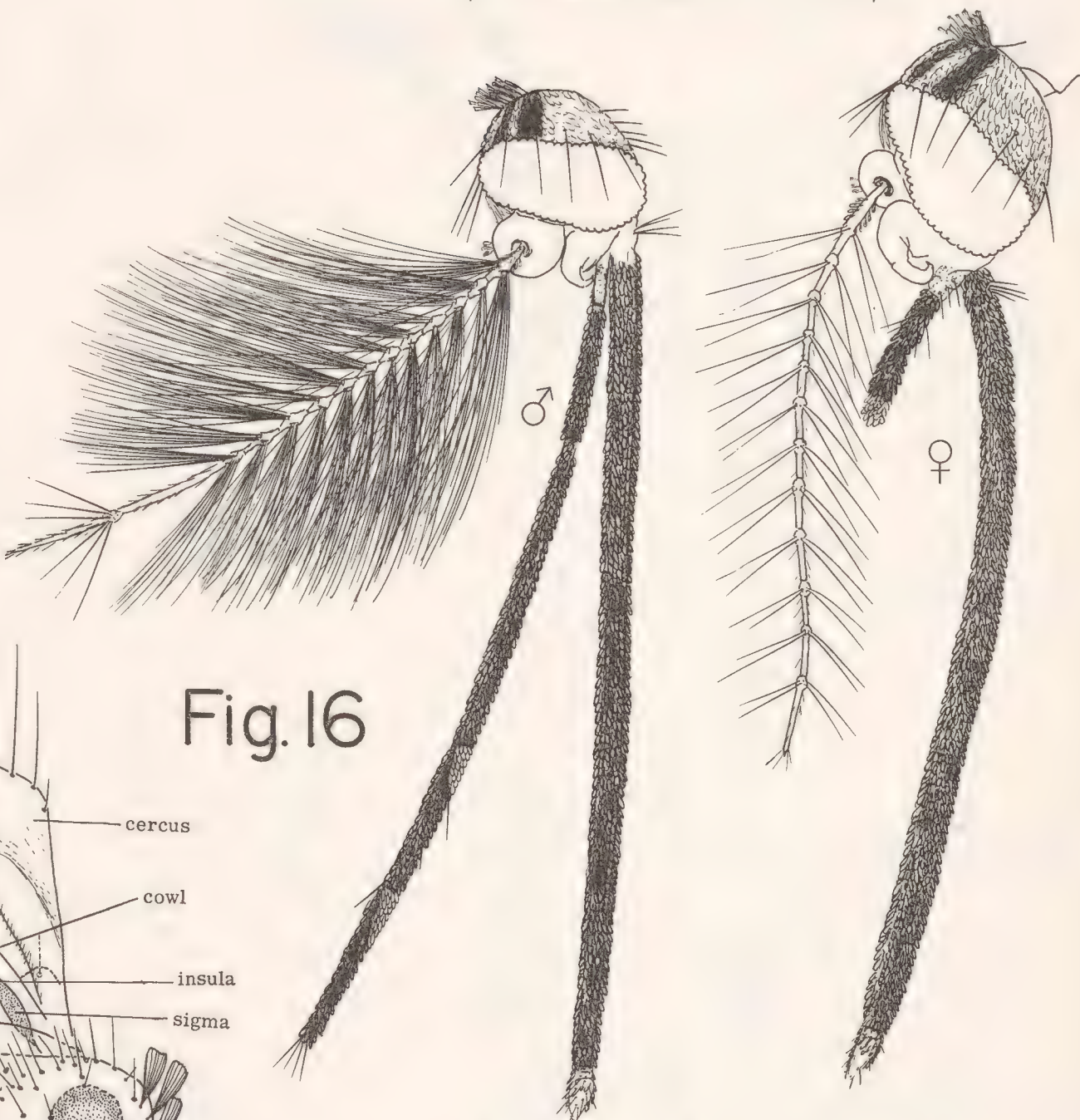
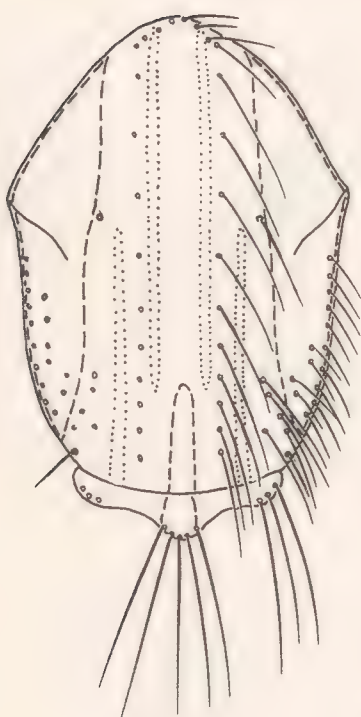
HOWARDINA



0.5

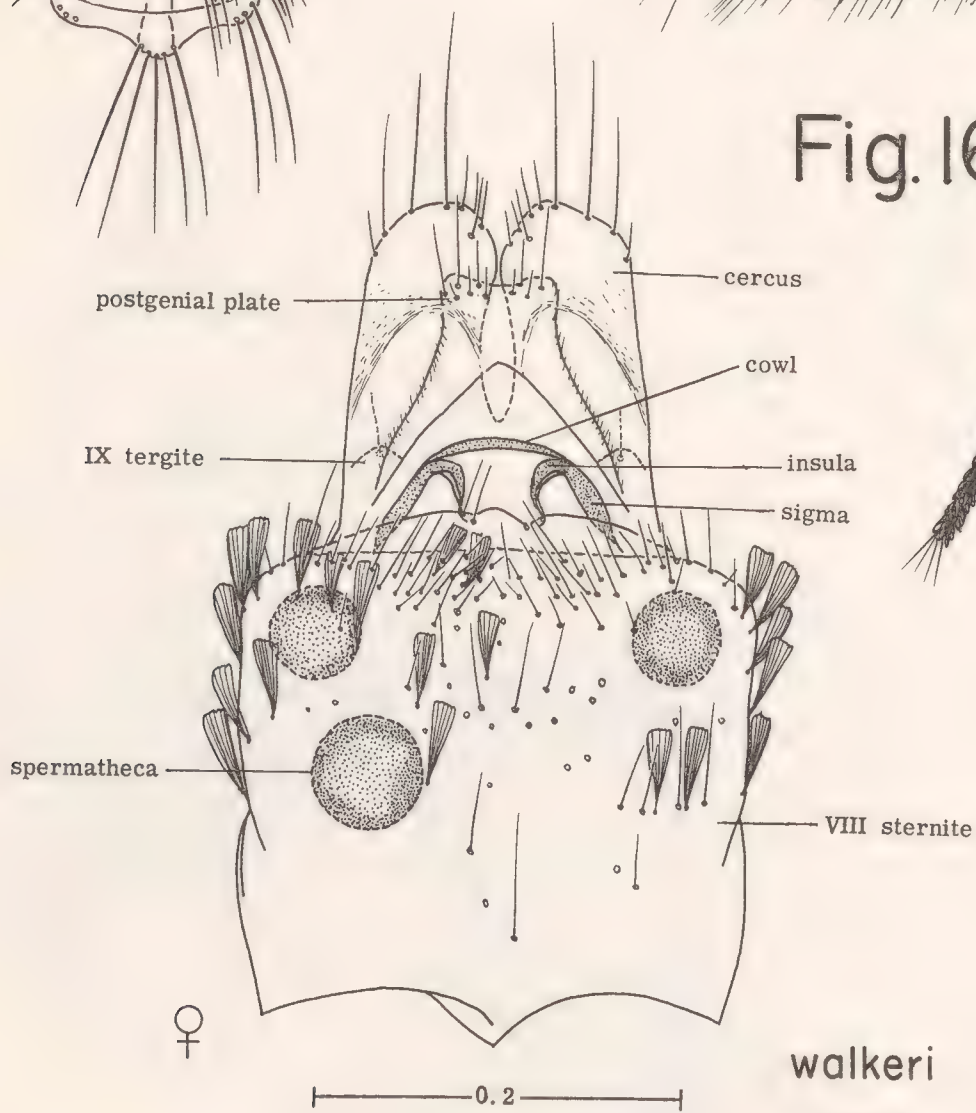


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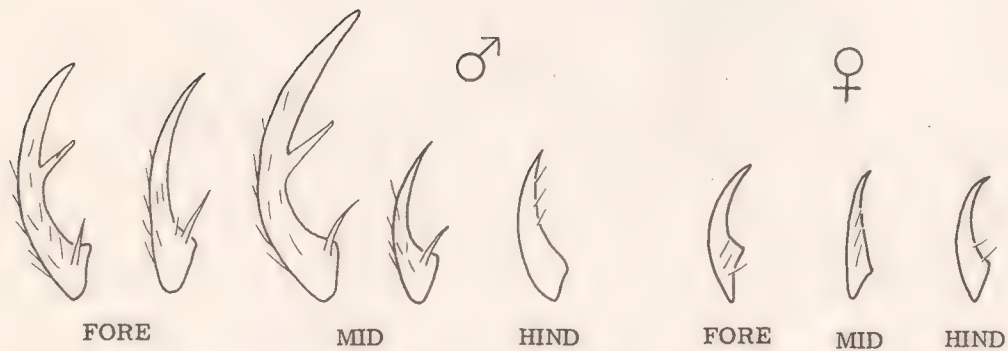
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Fig. 16



♀

walkeri
Jamaica



FORE

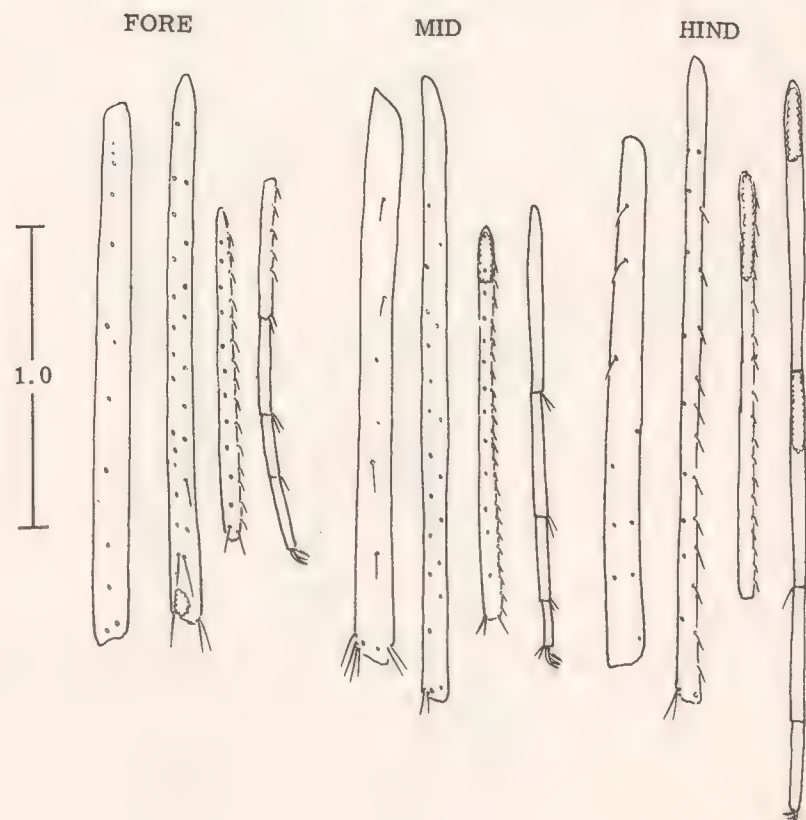
MID

HIND

FORE

MID

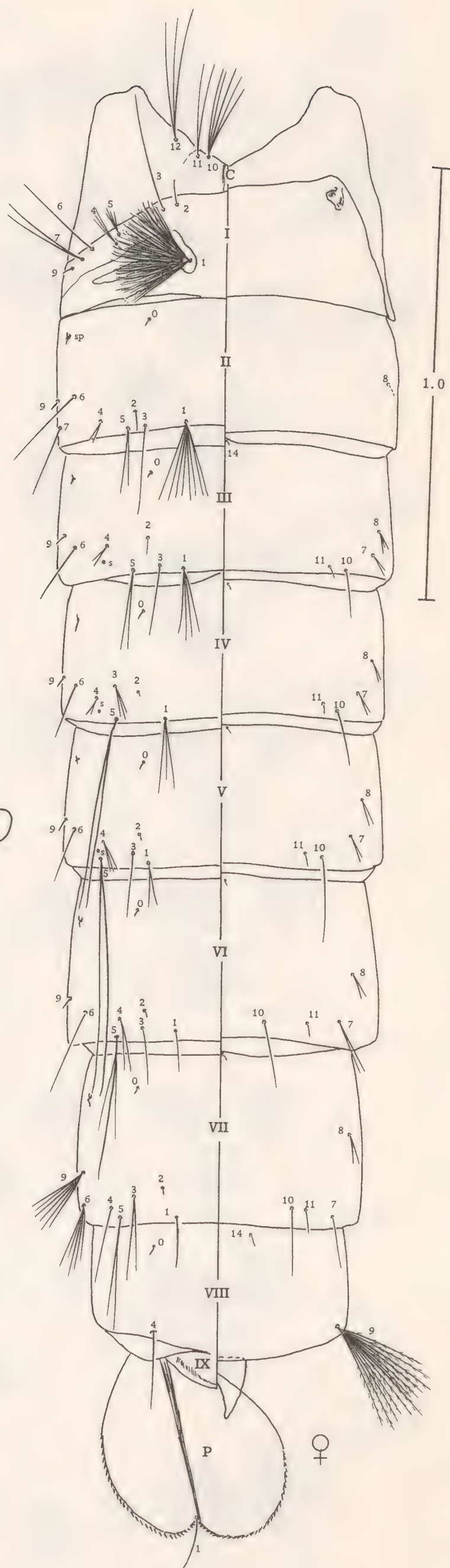
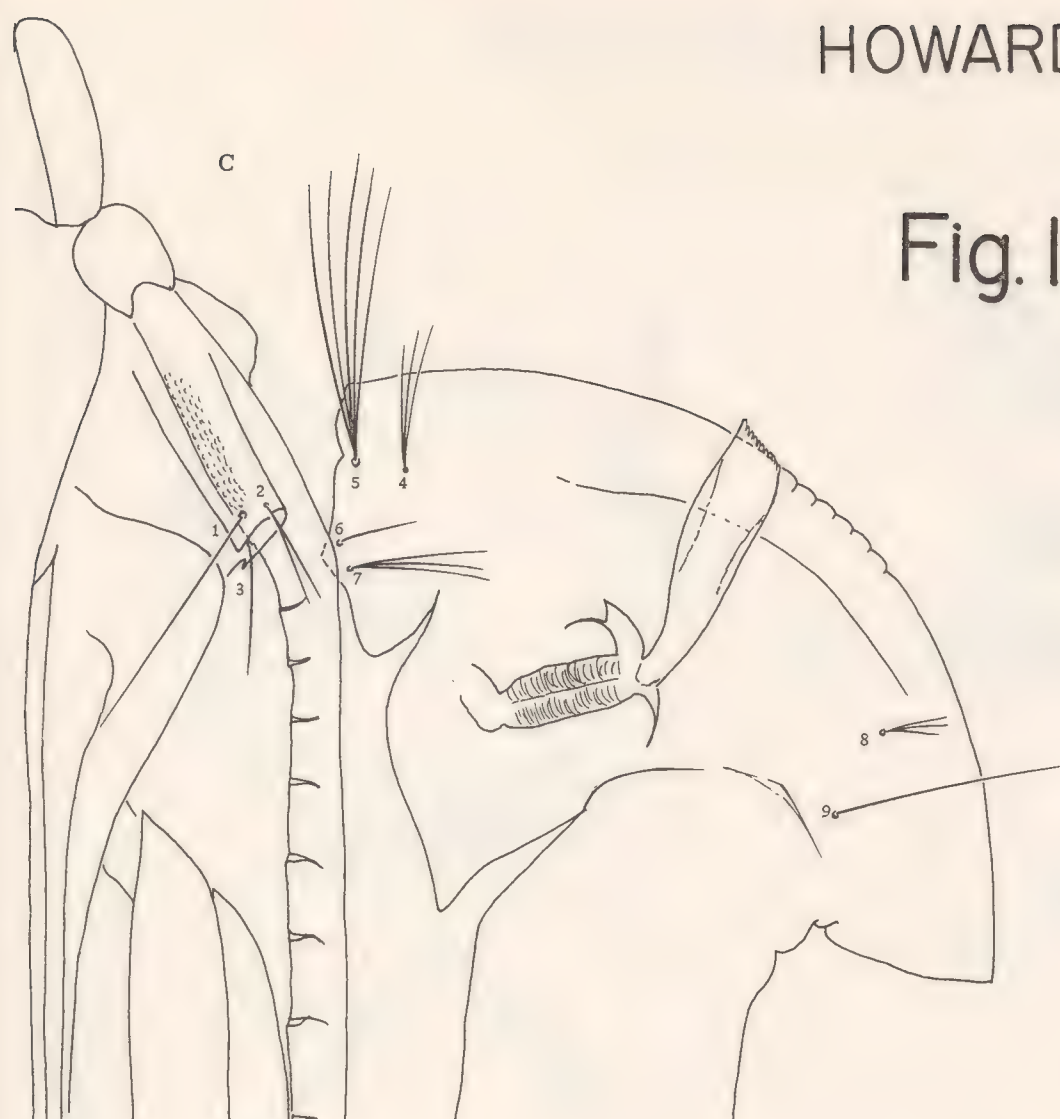
HIND



1.0

HOWARDINA

Fig. 17



walkeri

JA 379-10
Mt. Diablo
St. Ann
Jamaica

HOWARDINA

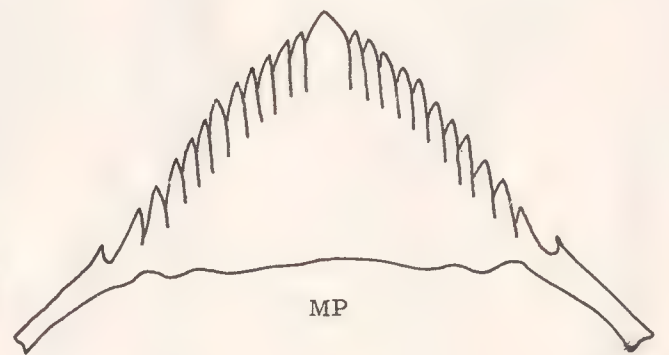
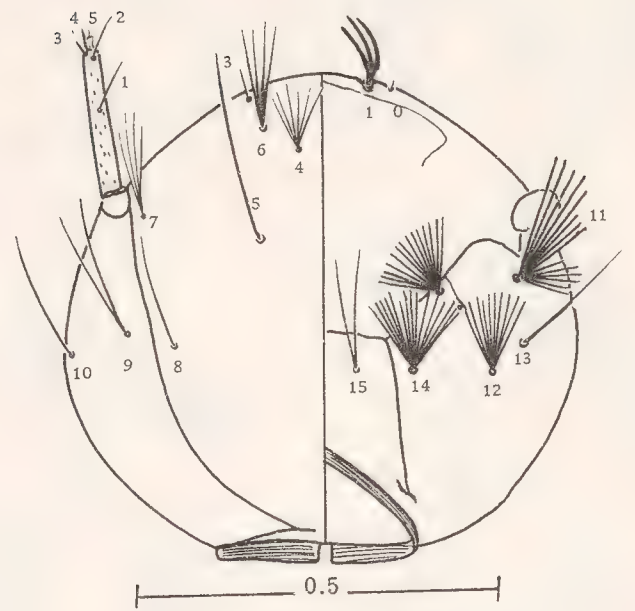
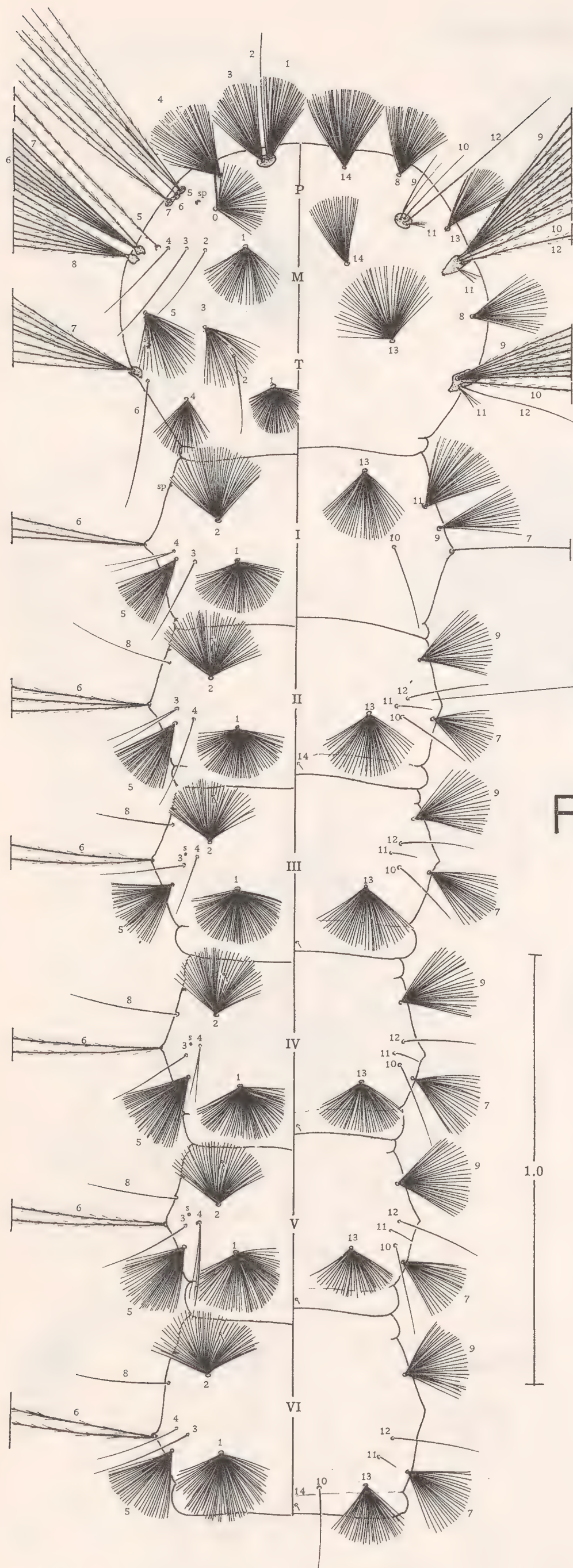
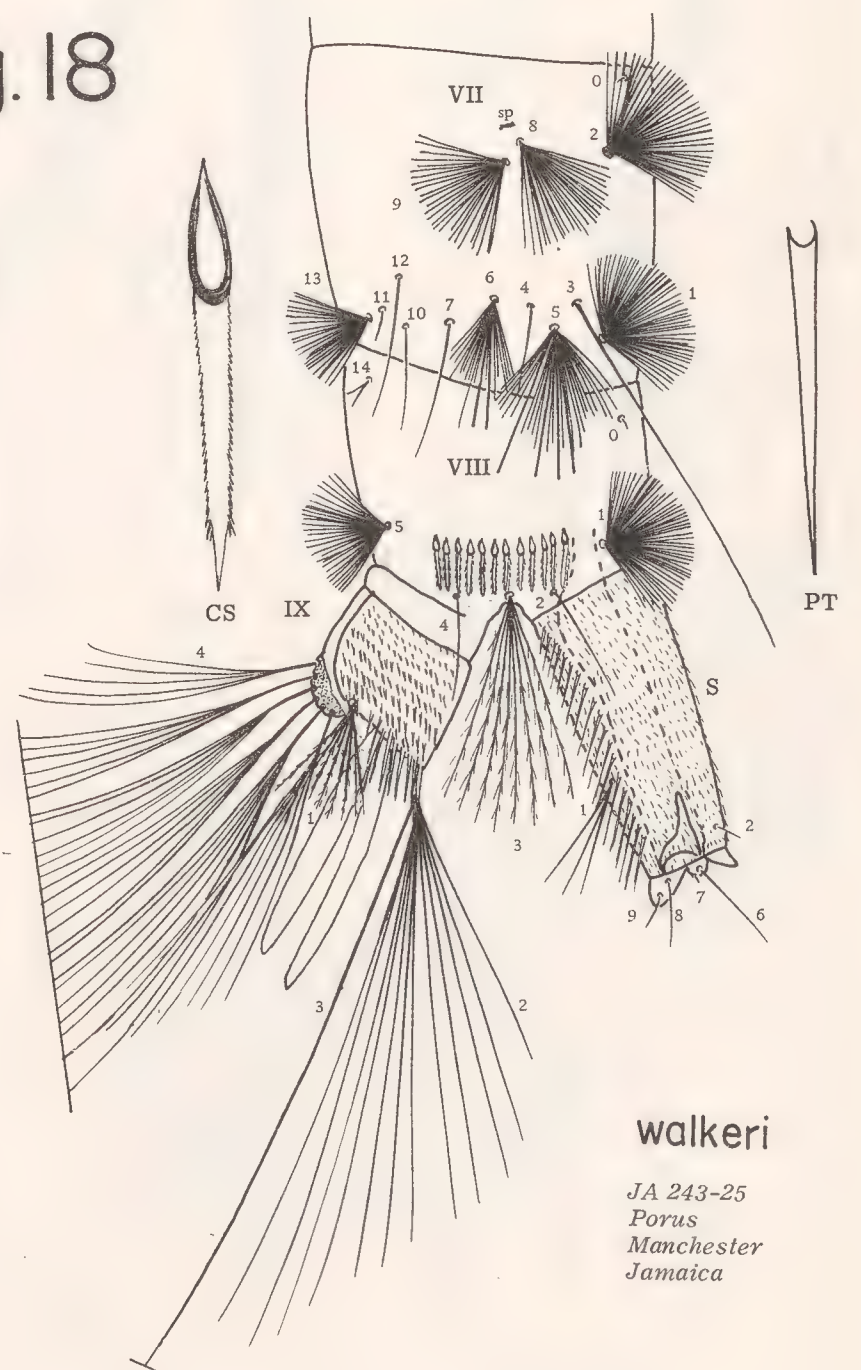


Fig. 18

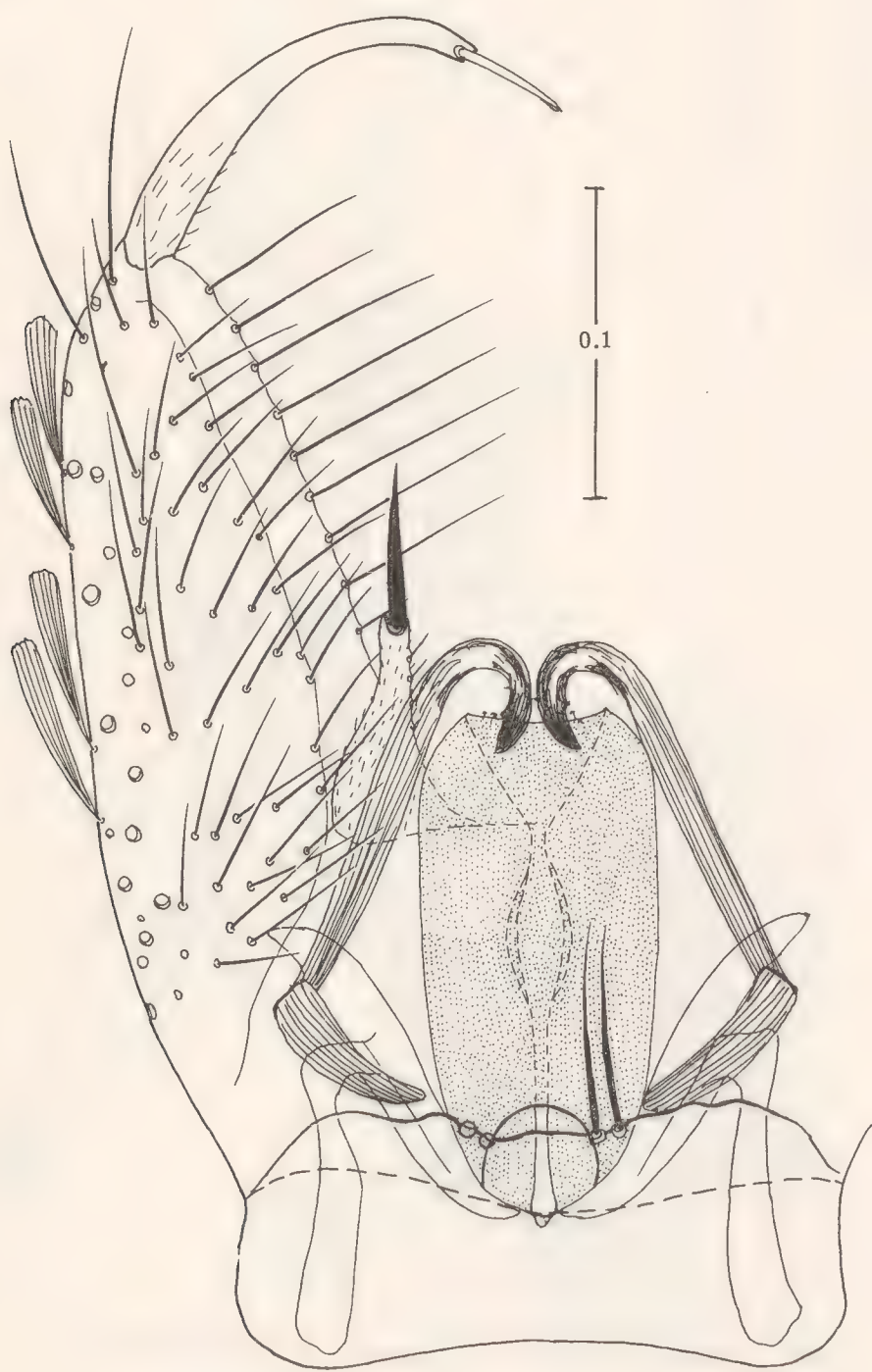
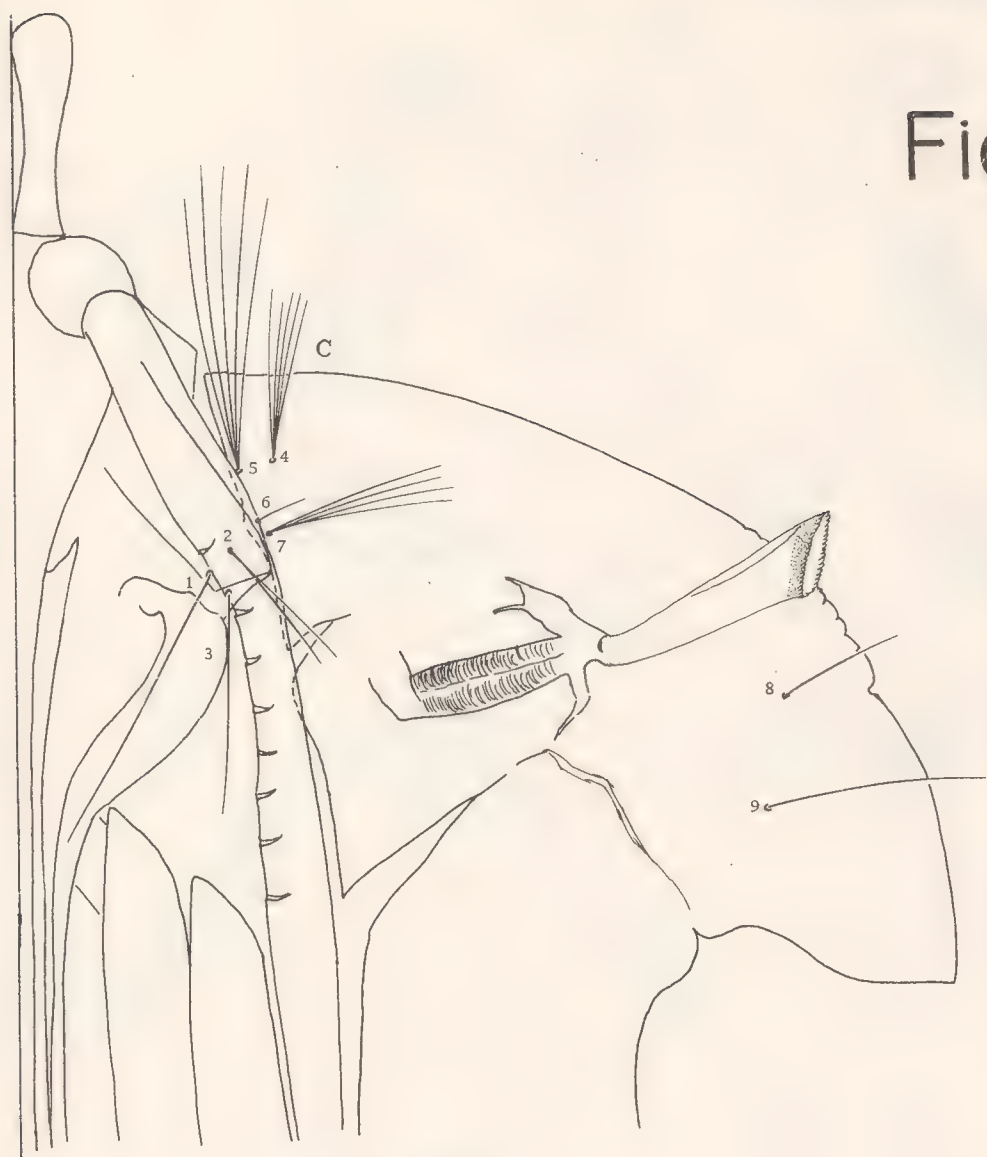


walkeri

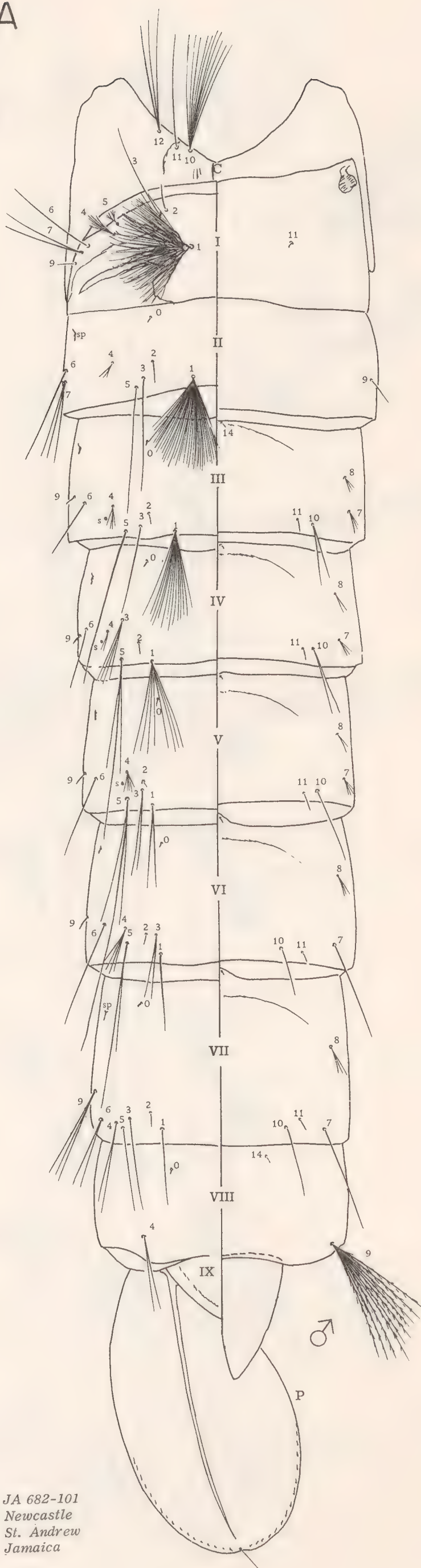
JA 243-25
Porus
Manchester
Jamaica

HOWARDINA

Fig. 19



aurites



JA 682-101
Newcastle
St. Andrew
Jamaica

HOWARDINA

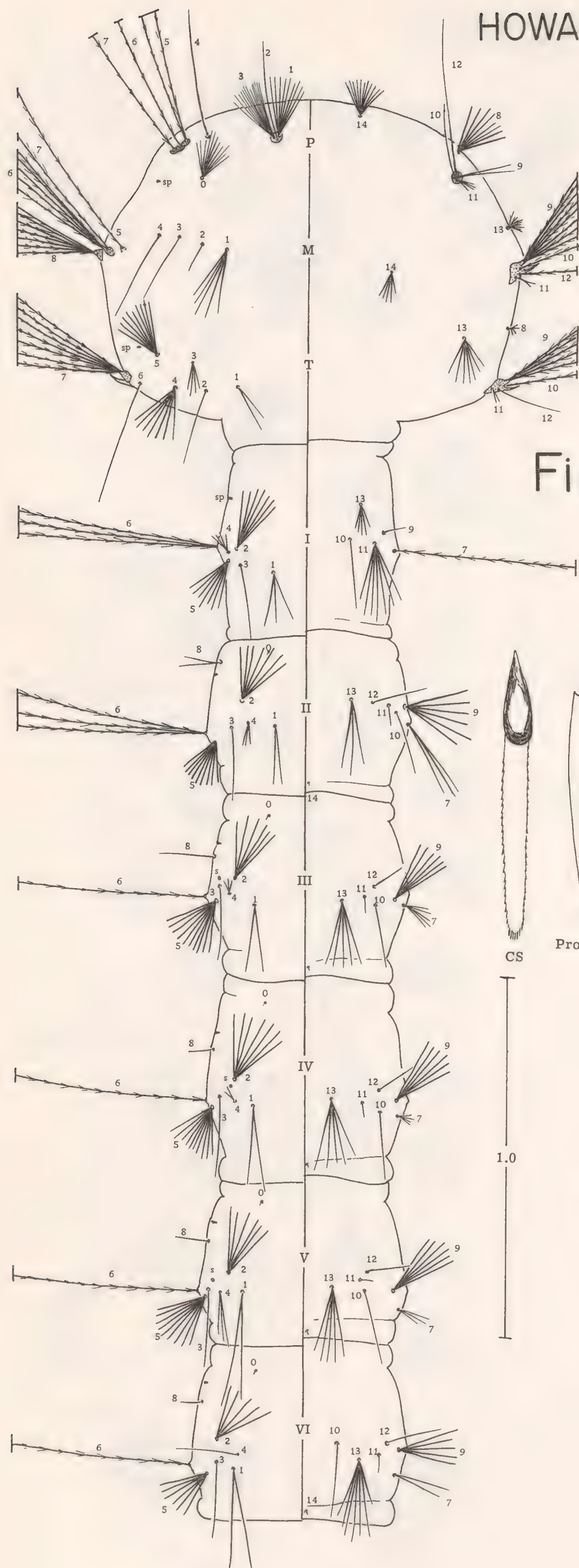
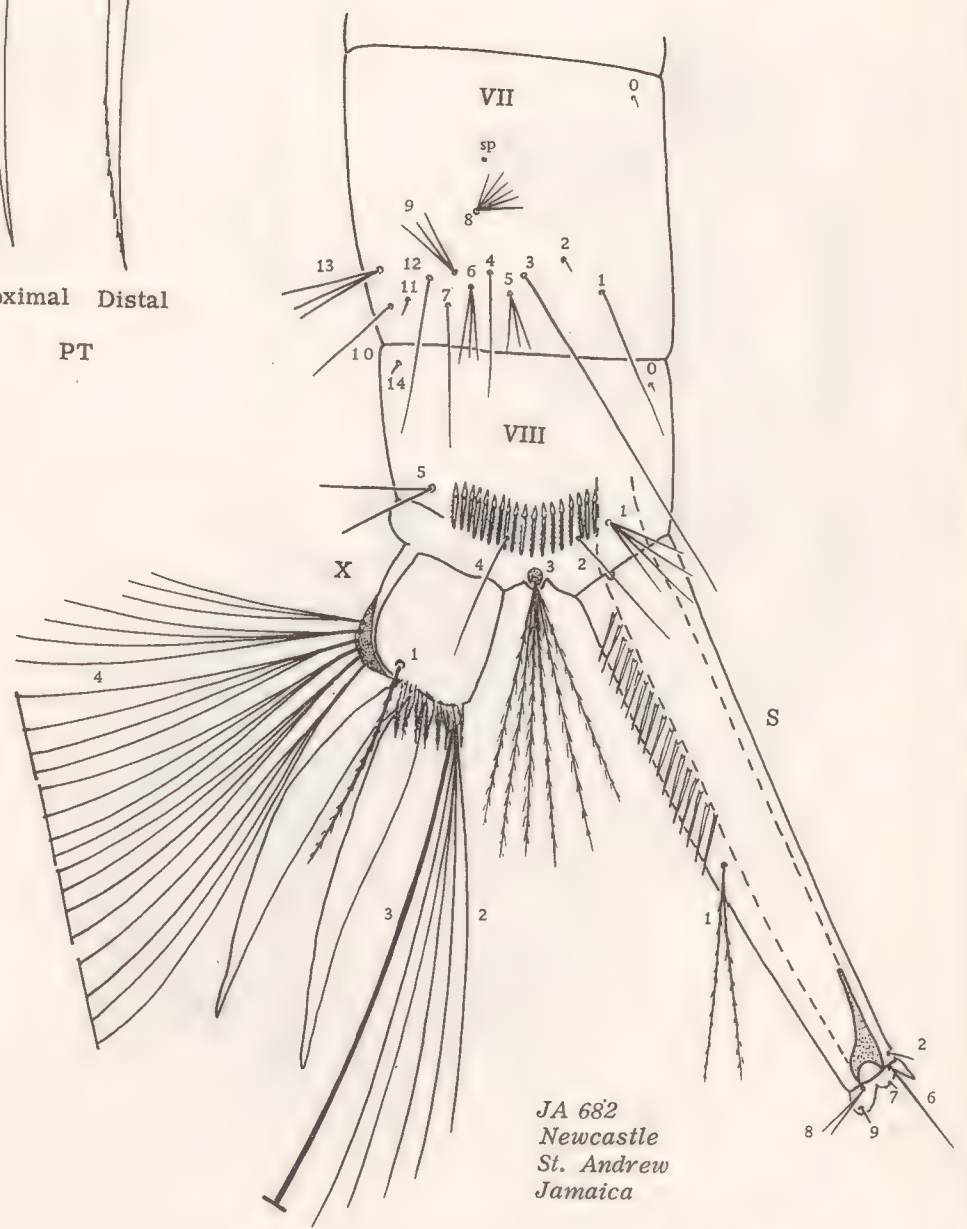
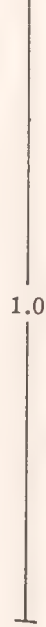
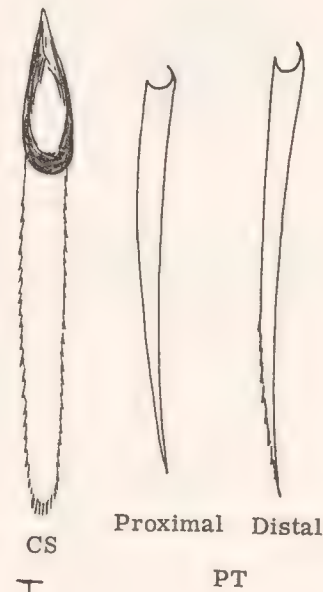
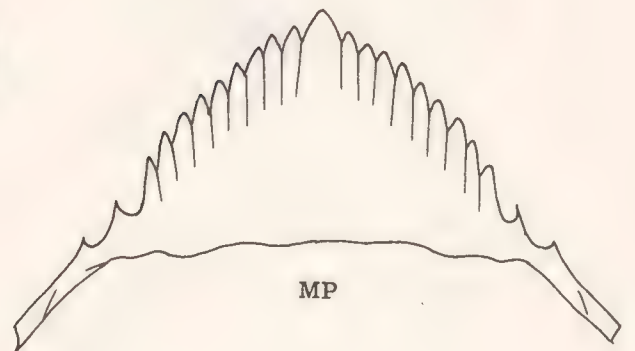
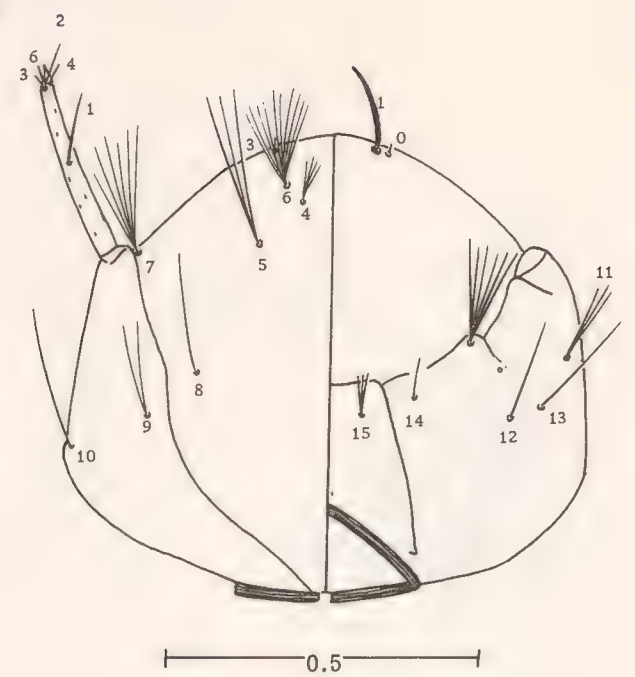


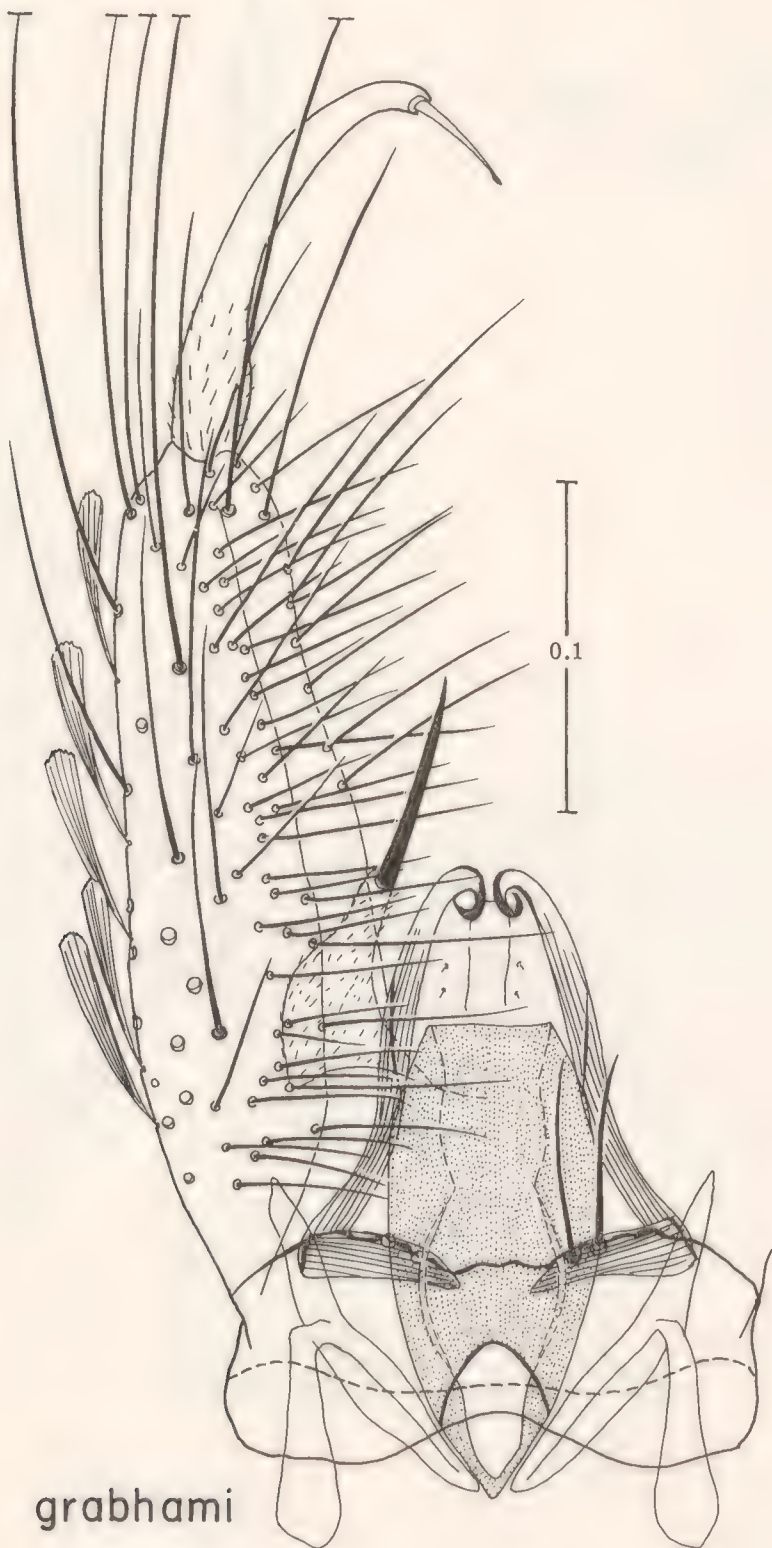
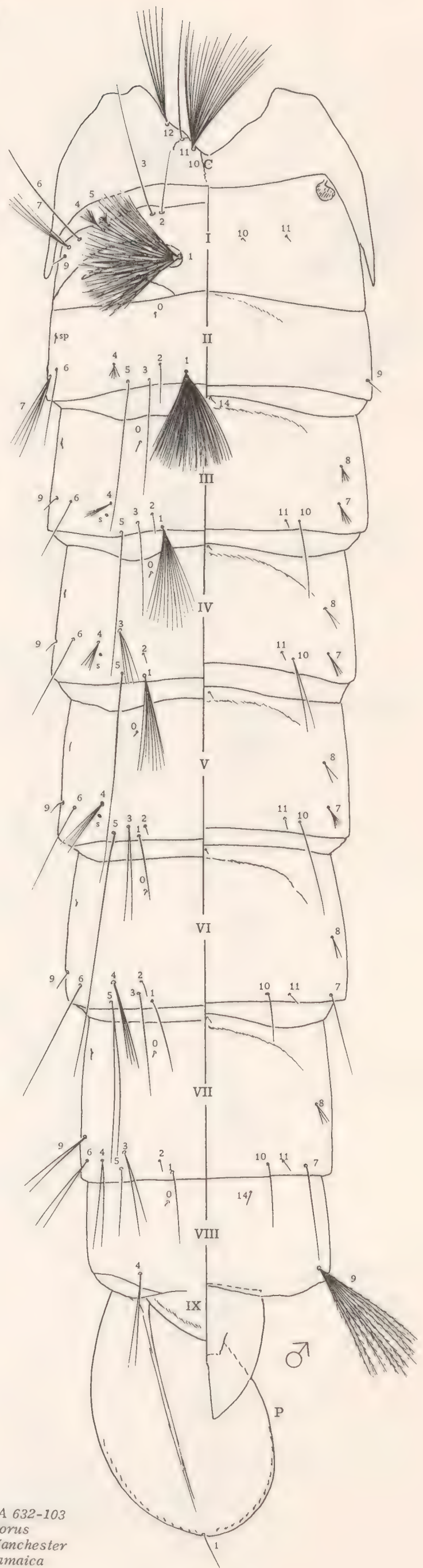
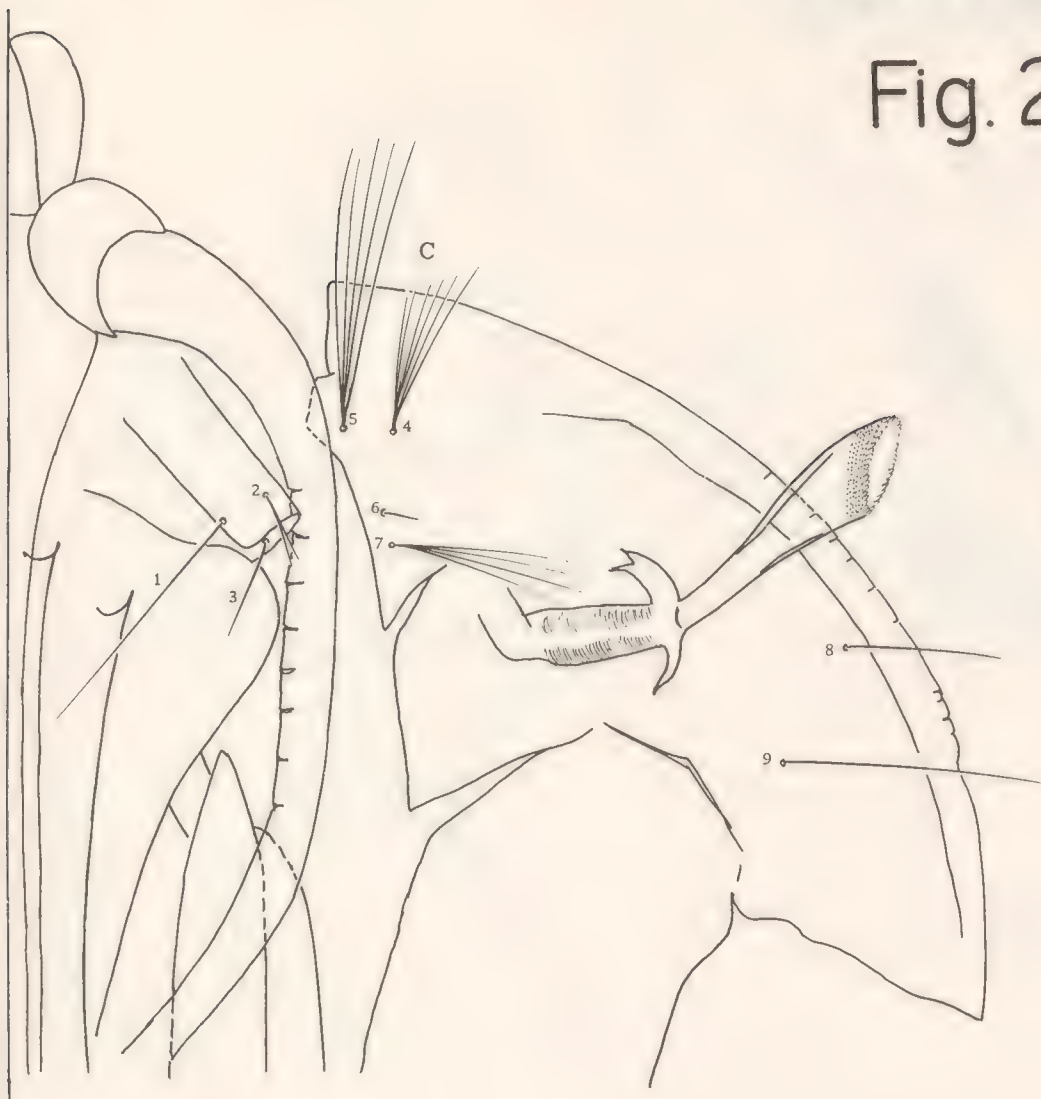
Fig. 20



aurites

HOWARDINA

Fig. 21



grabhami

JA 632-103
Porus
Manchester
Jamaica

HOWARDINA

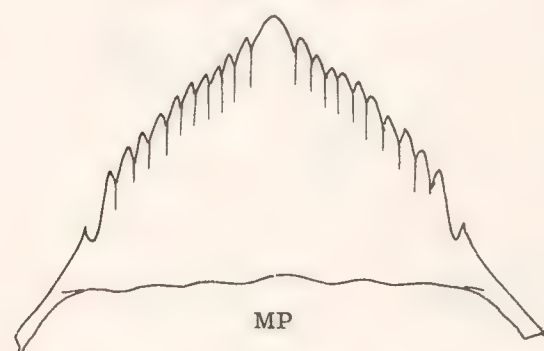
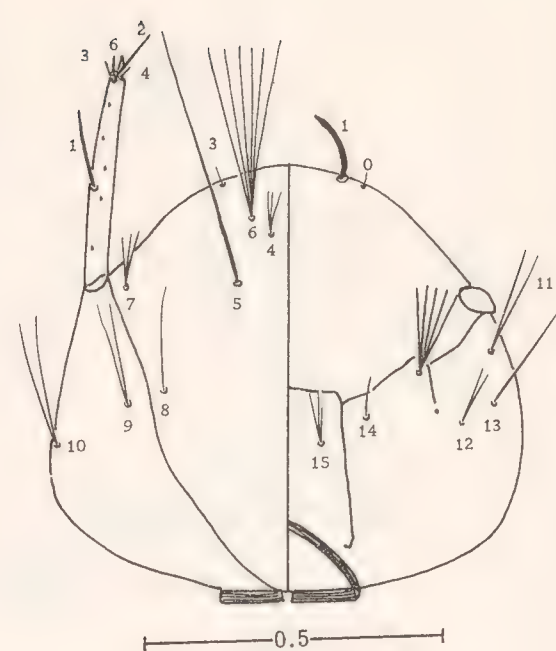
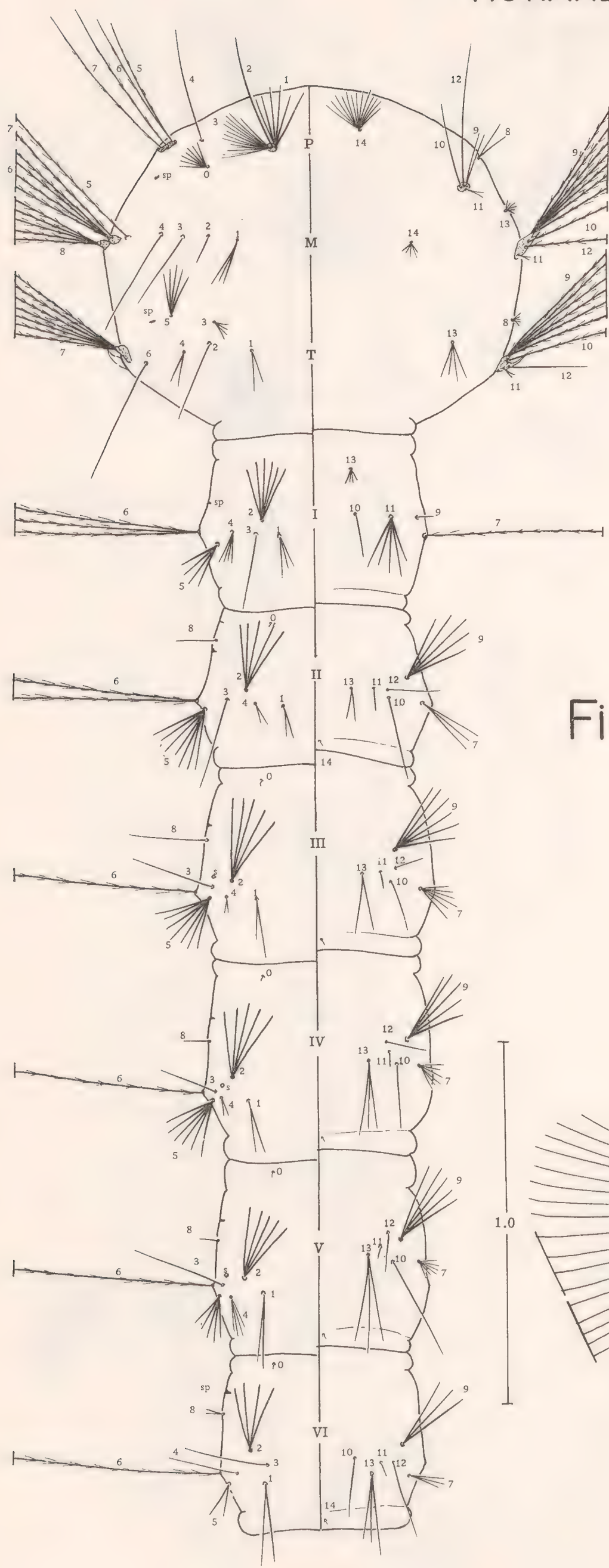
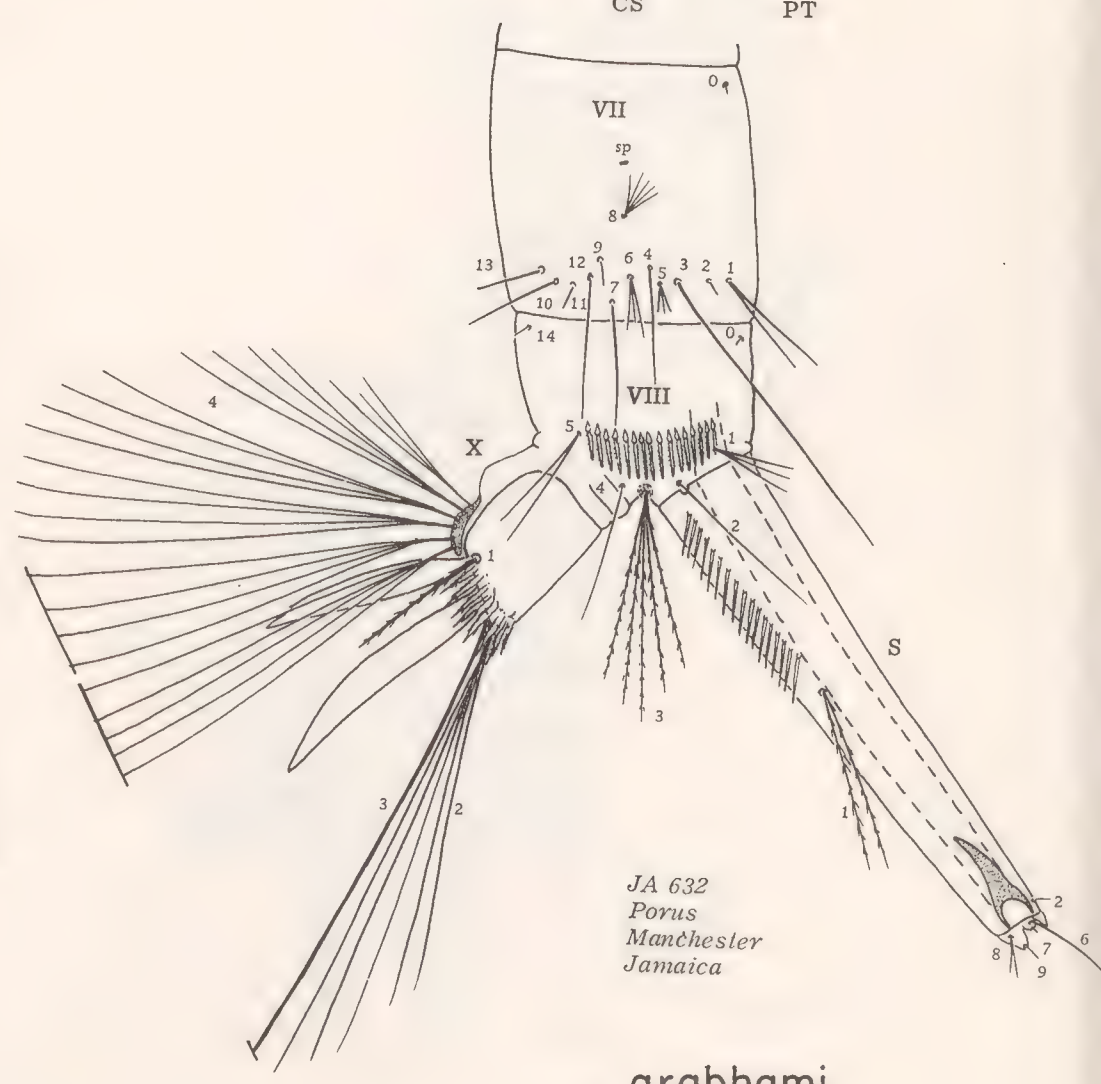


Fig. 22

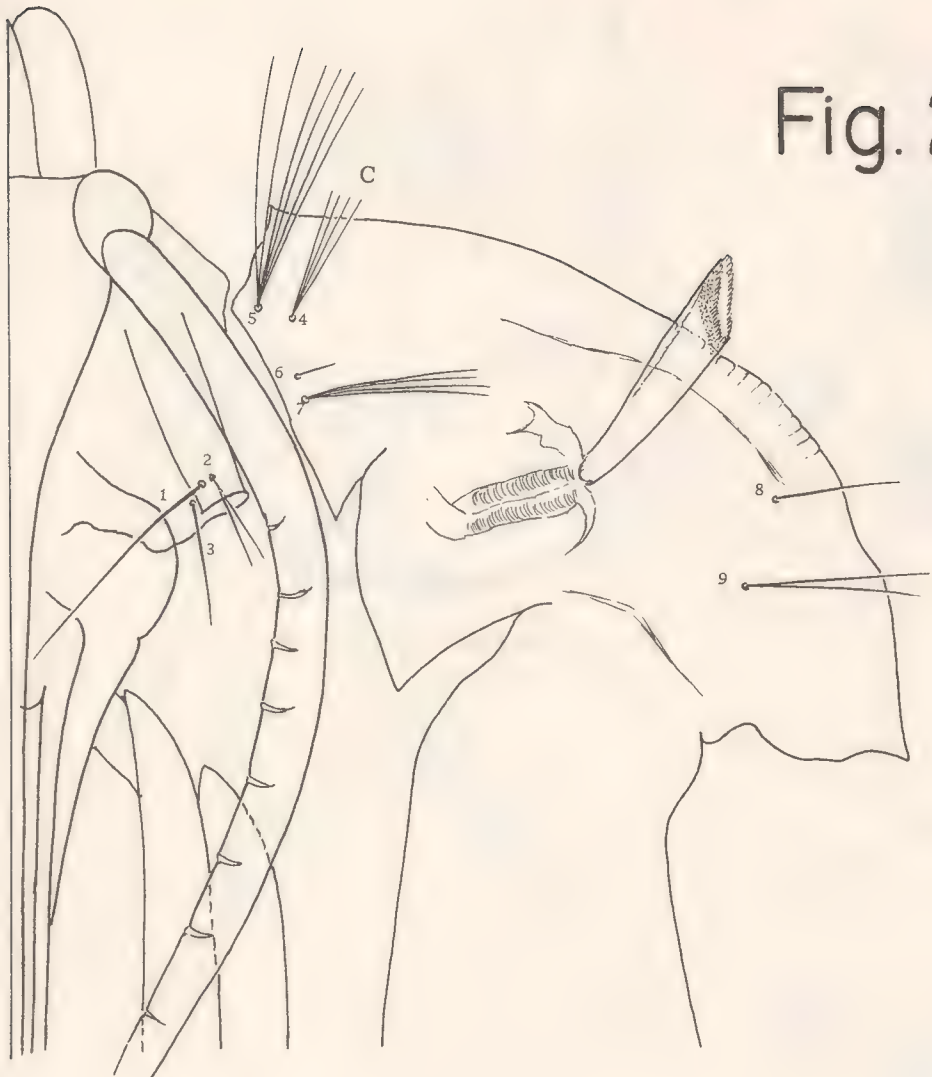


JA 632
Porus
Manchester
Jamaica

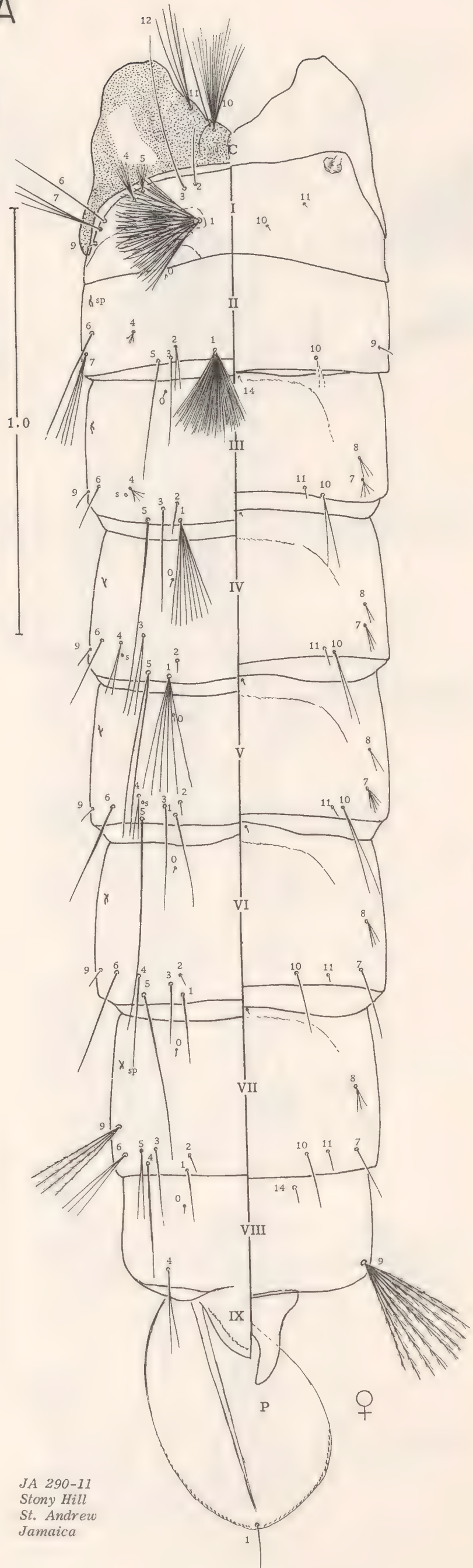
grabhami

HOWARDINA

Fig. 23



inaequalis



JA 290-11
Stony Hill
St. Andrew
Jamaica

HOWARDINA

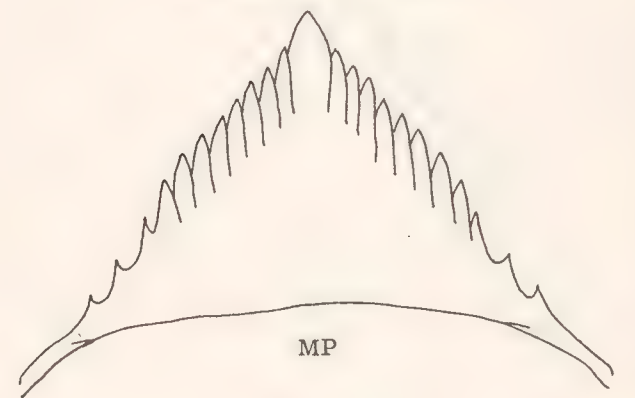
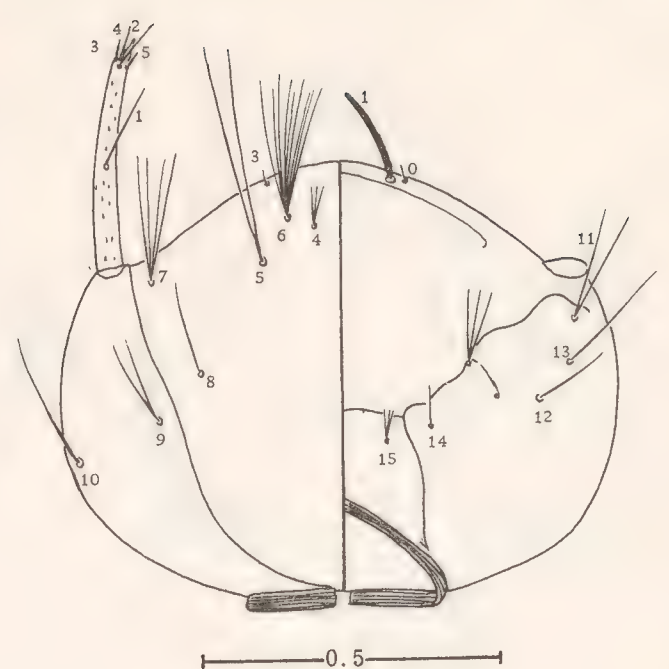
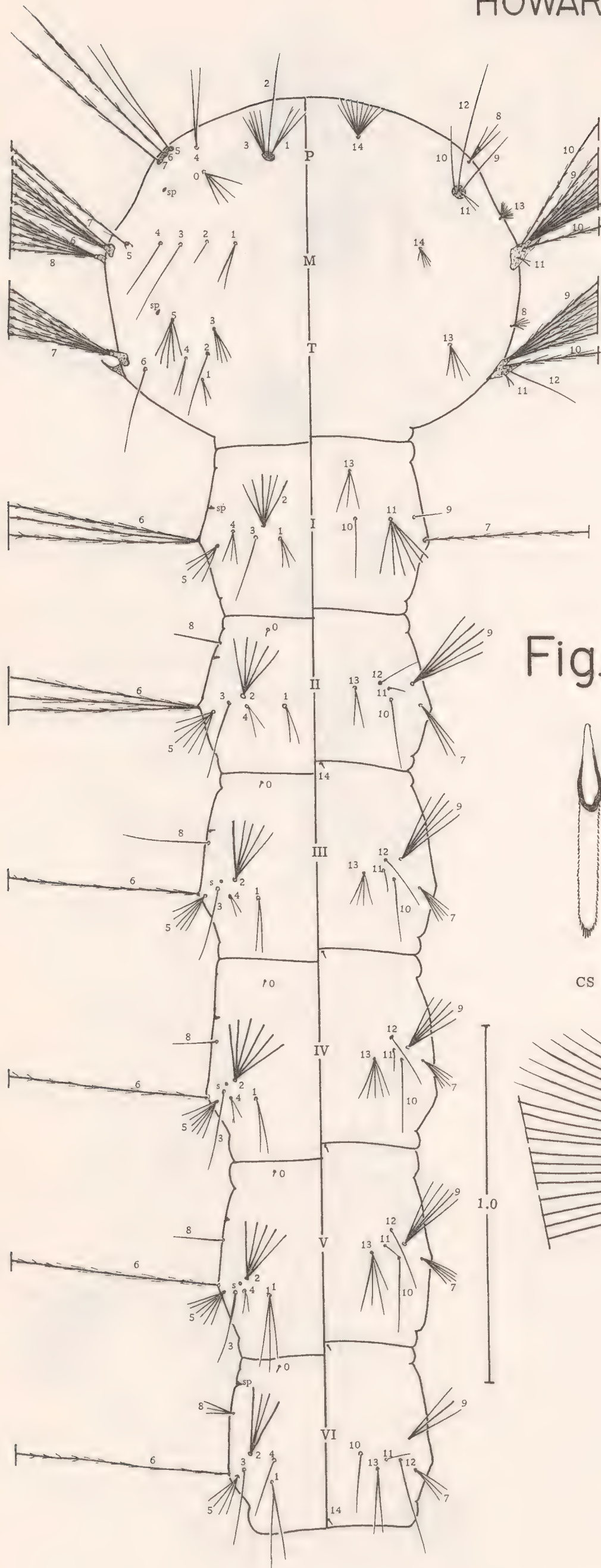
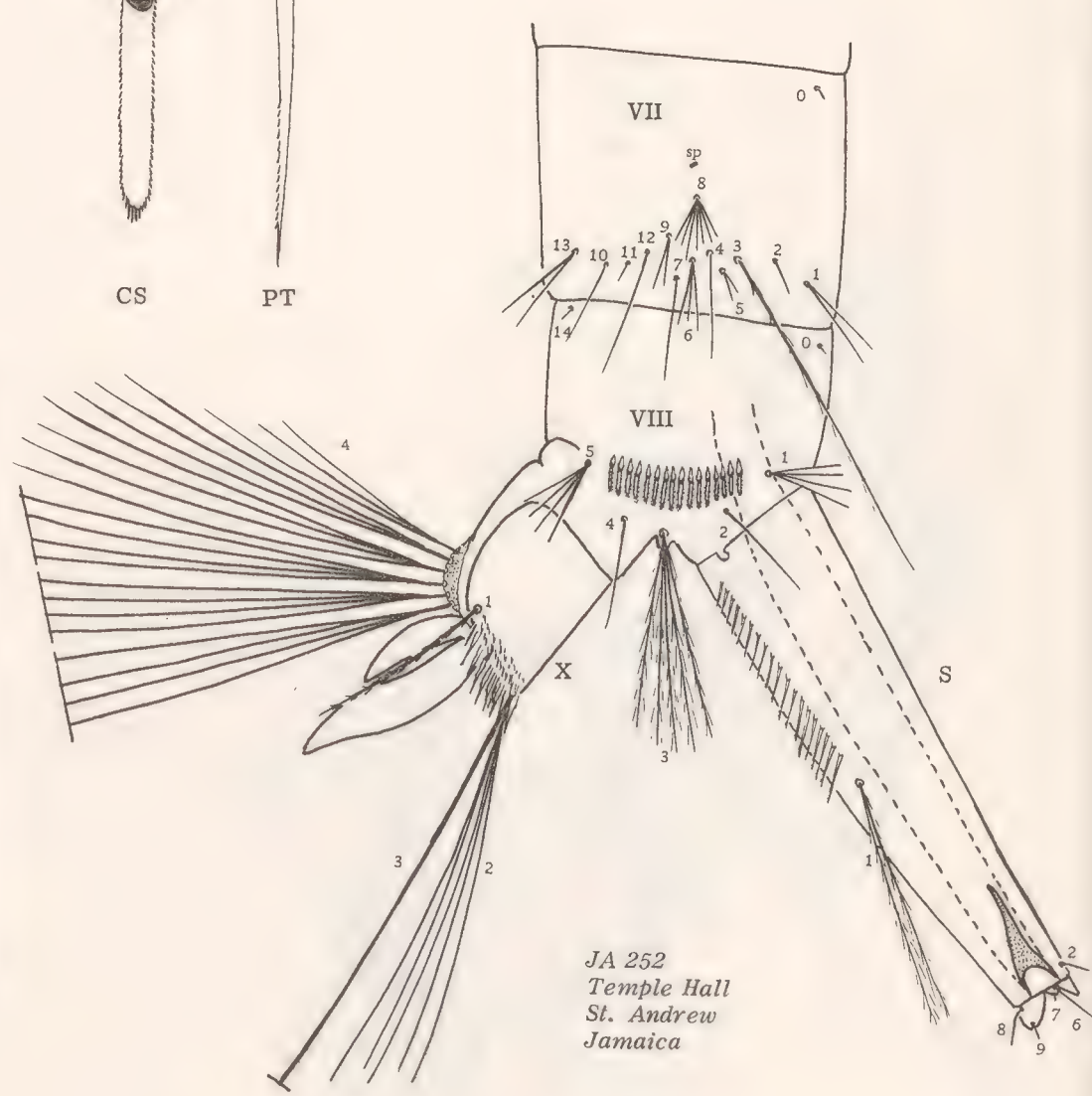
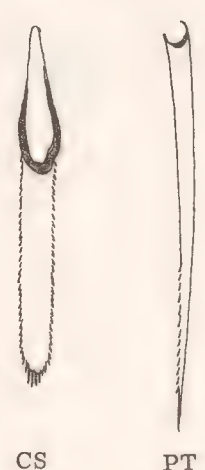


Fig. 24

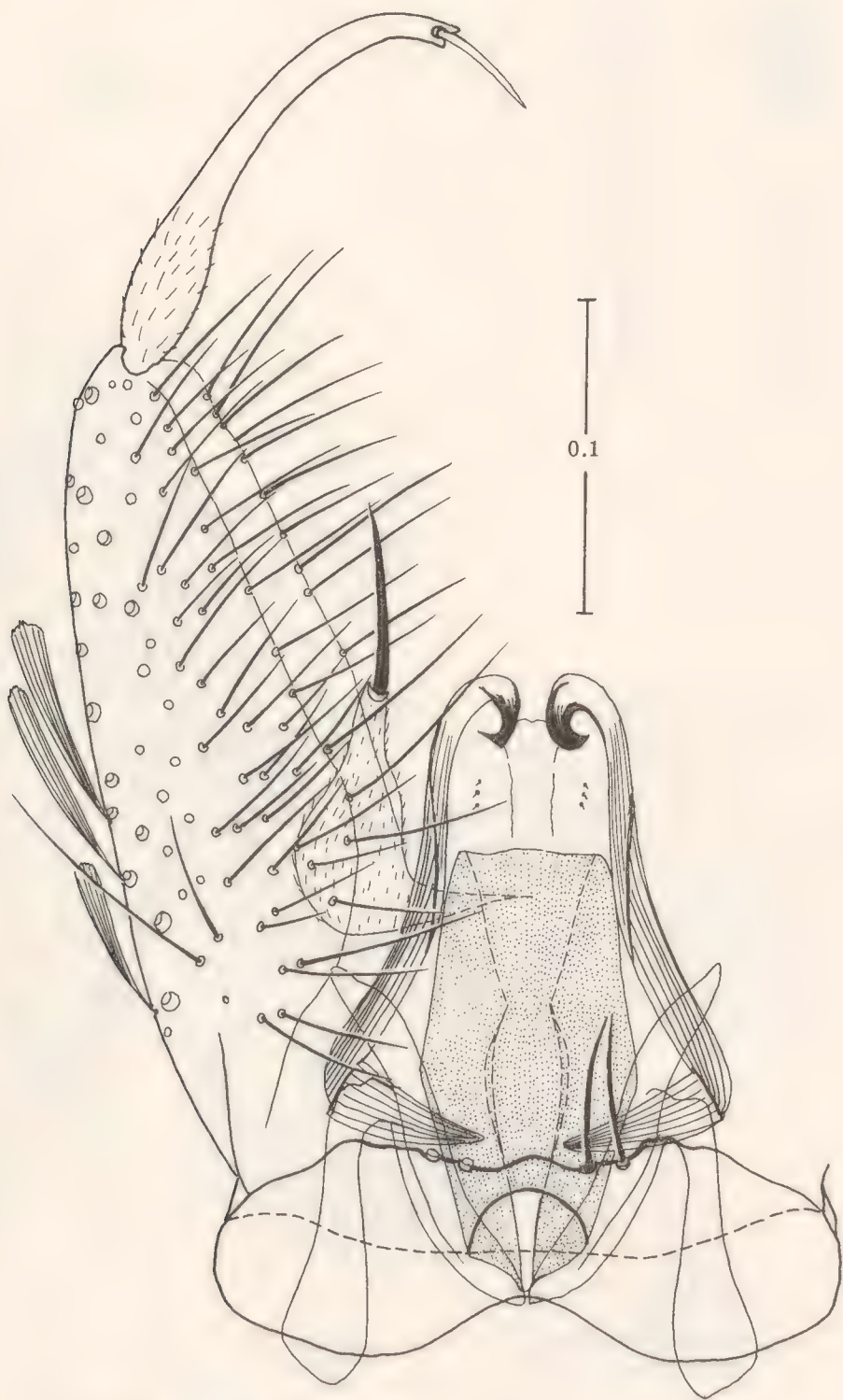
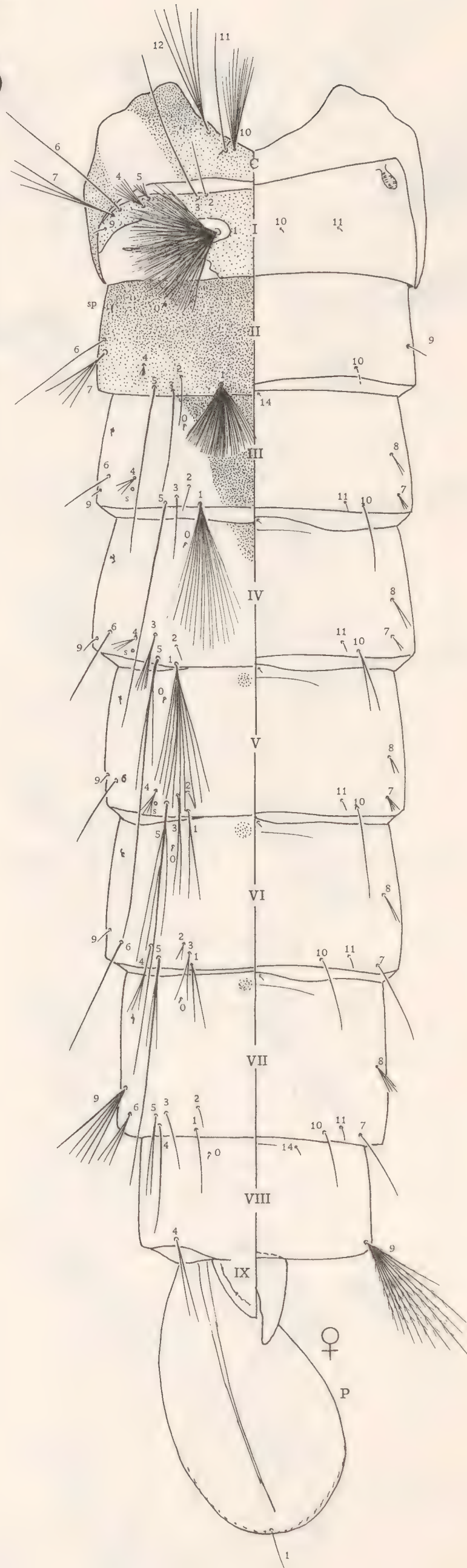


JA 252
Temple Hall
St. Andrew
Jamaica

inaequalis

HOWARDINA

Fig. 25



stenei Hope Farm
Porus, Manchester

HOWARDINA

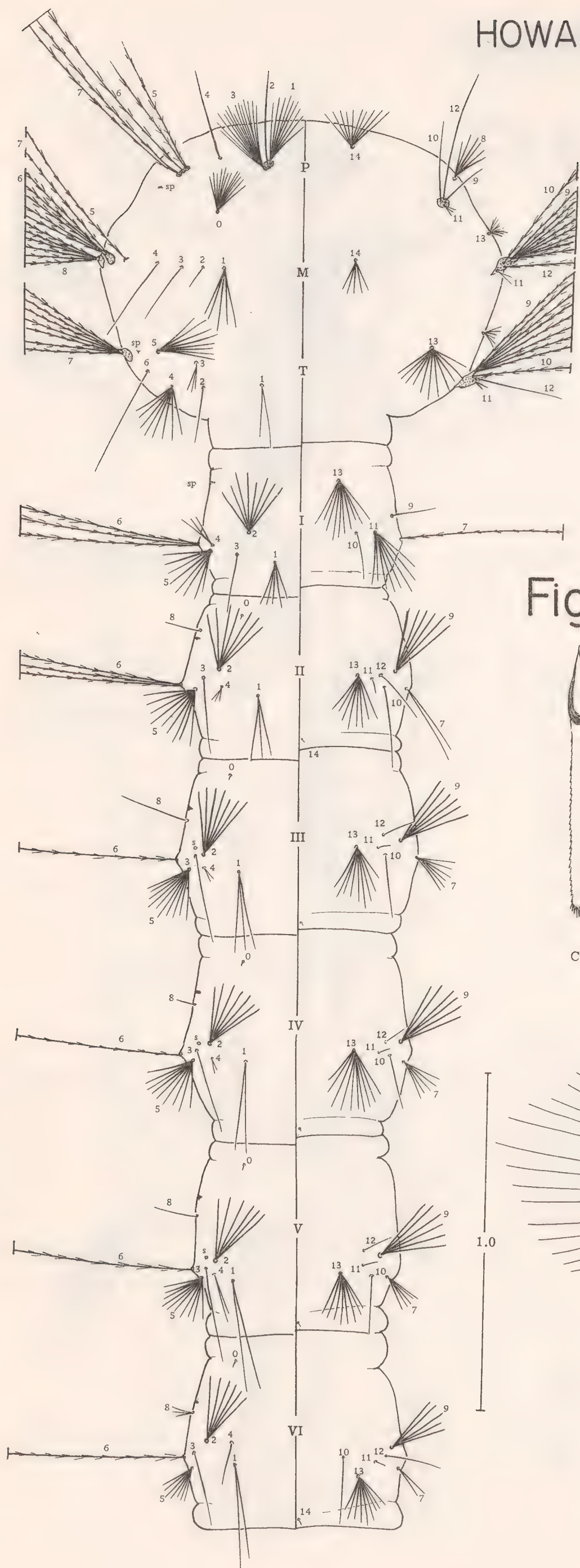
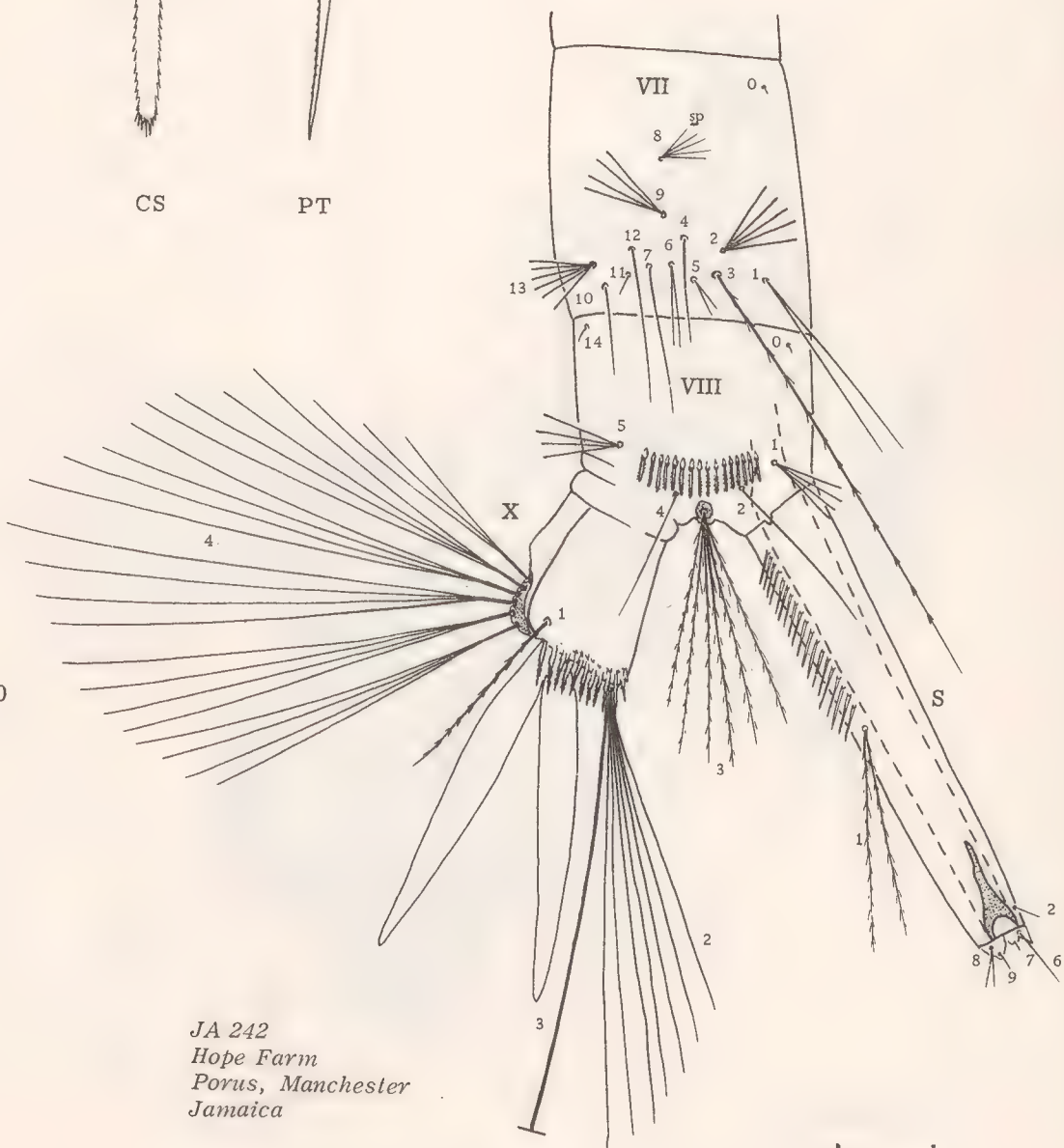
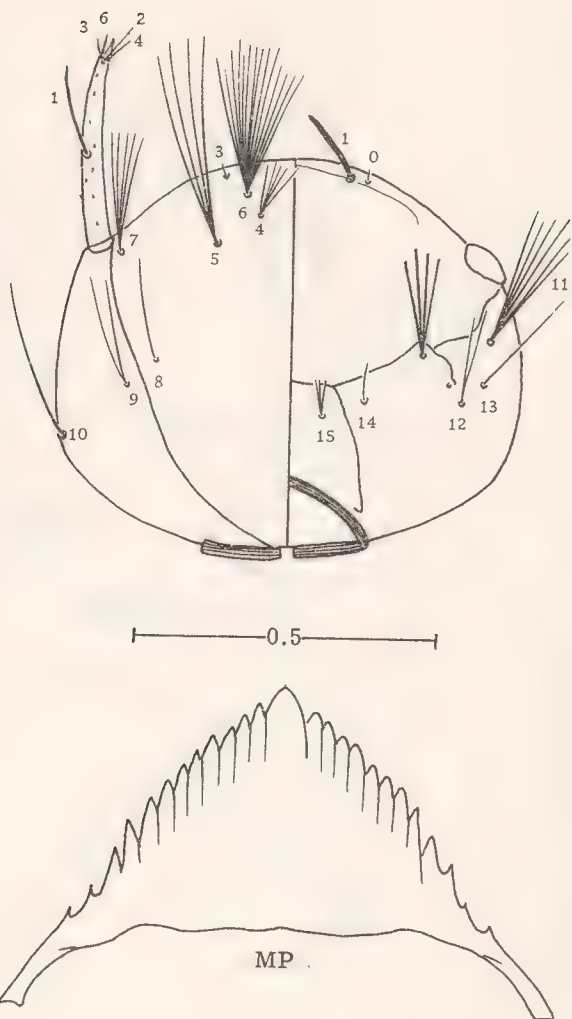
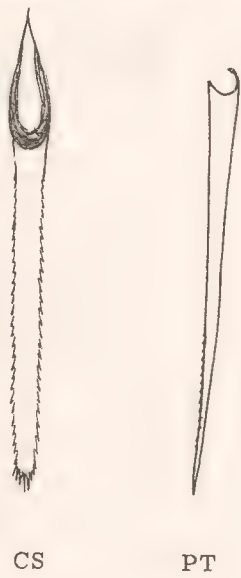


Fig. 26

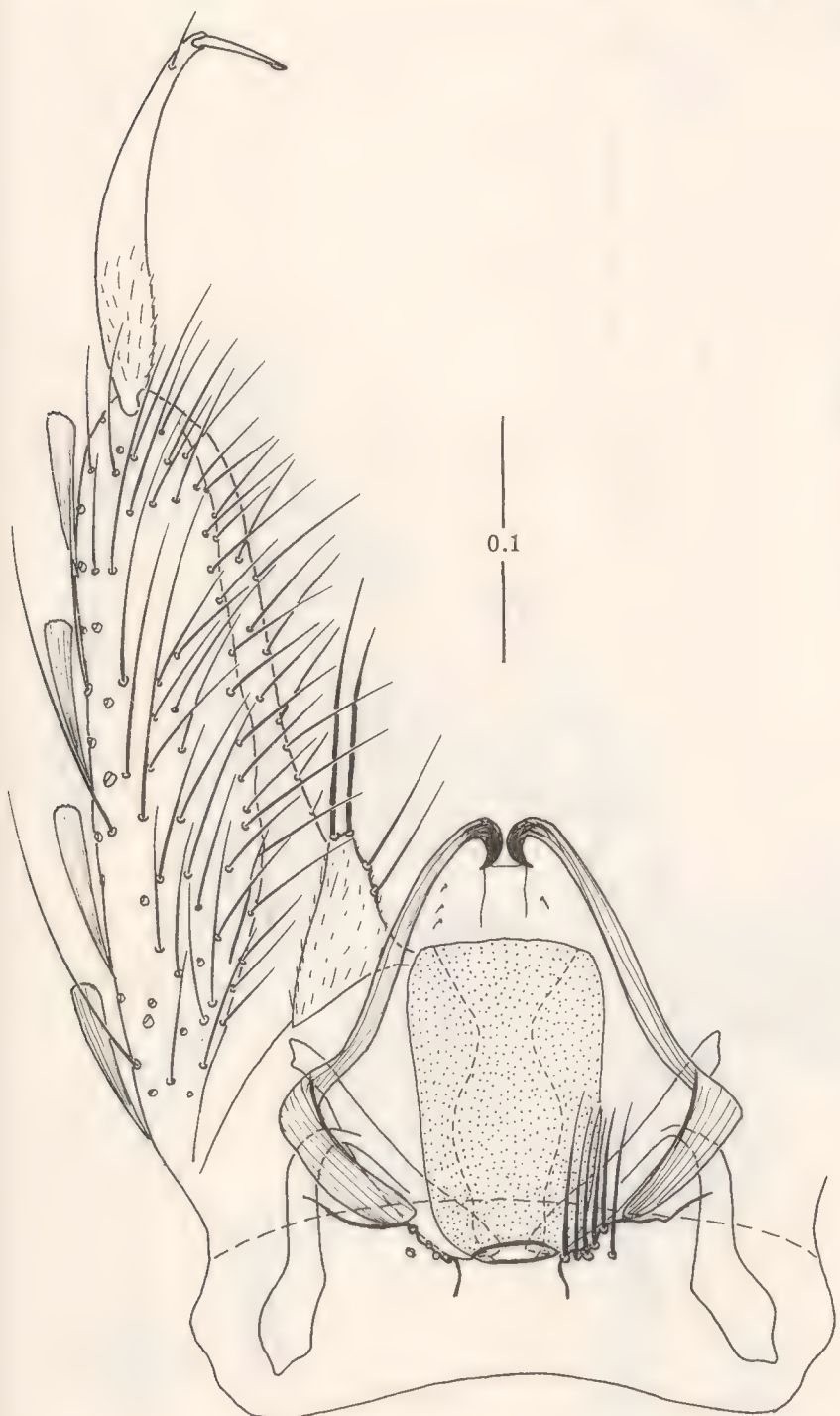
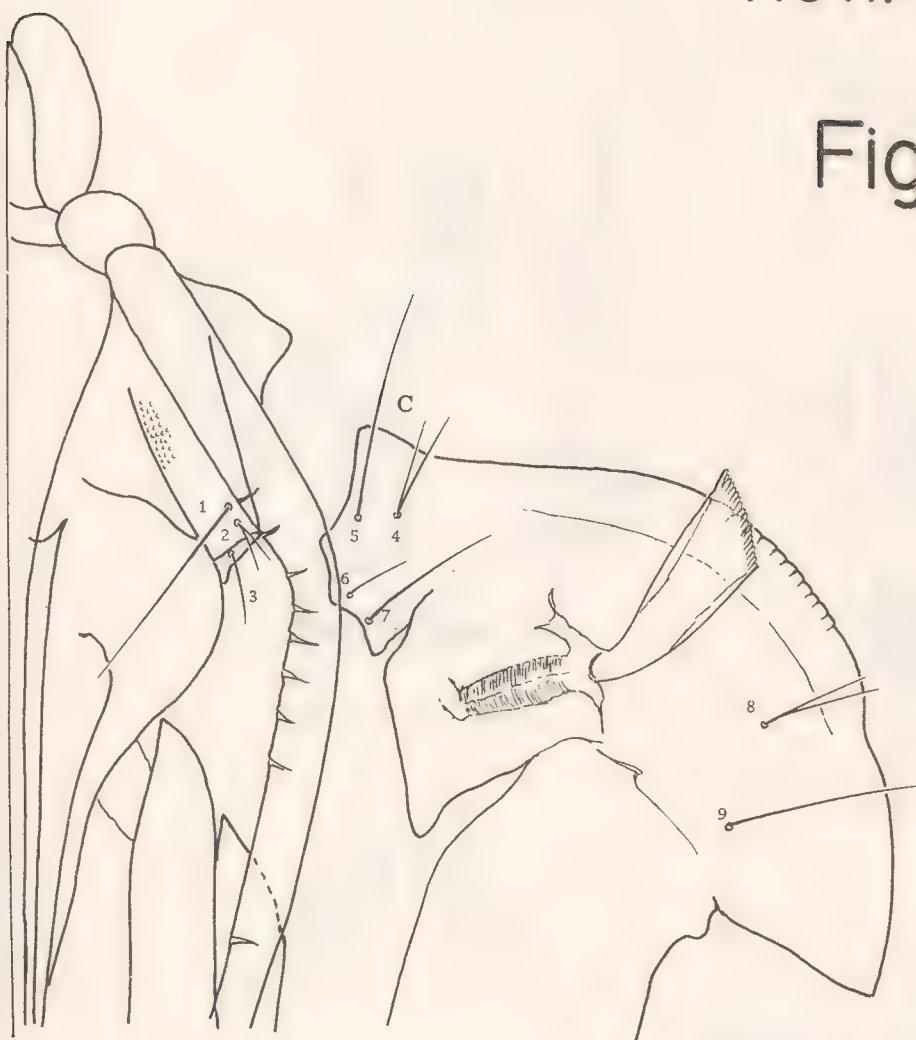


JA 242
Hope Farm
Porus, Manchester
Jamaica

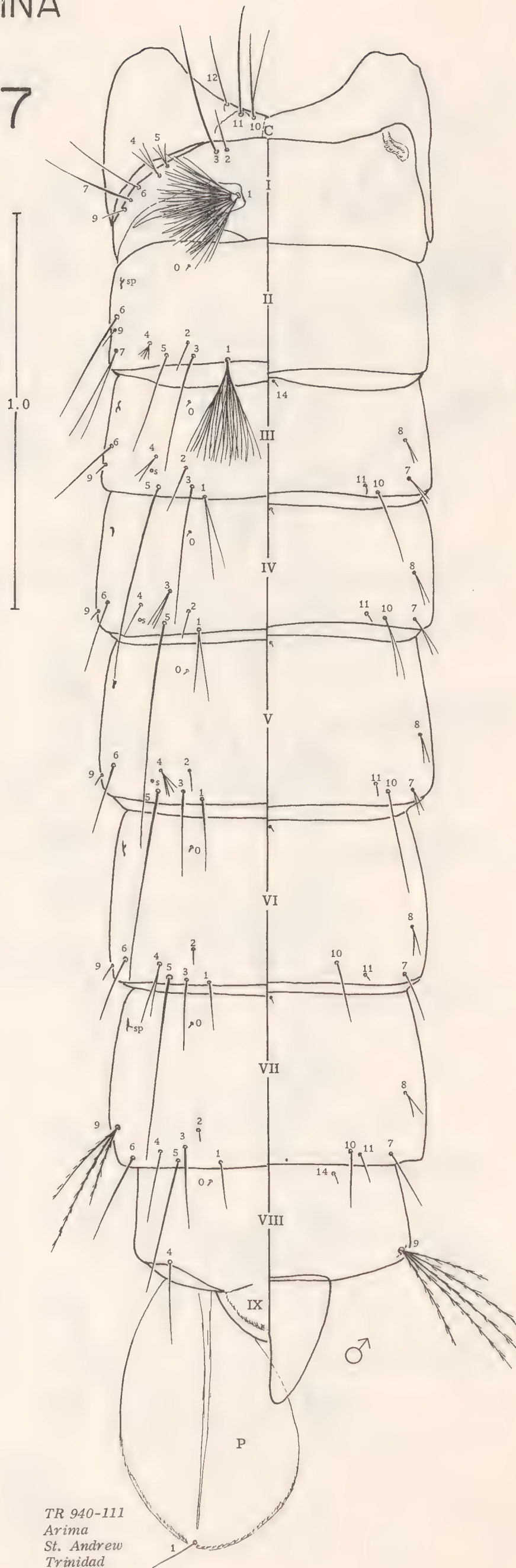
stenei

HOWARDINA

Fig. 27

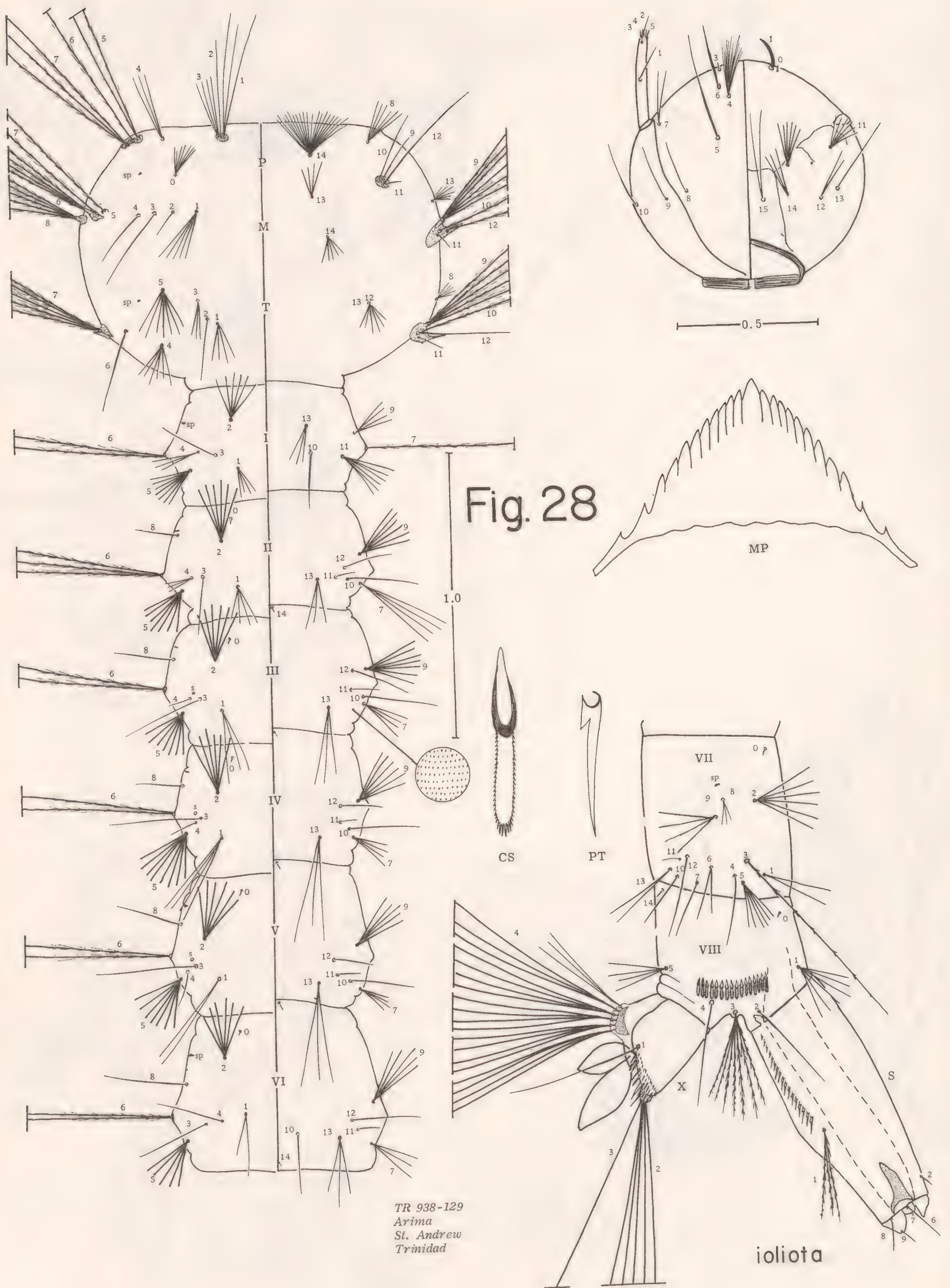


ioliota



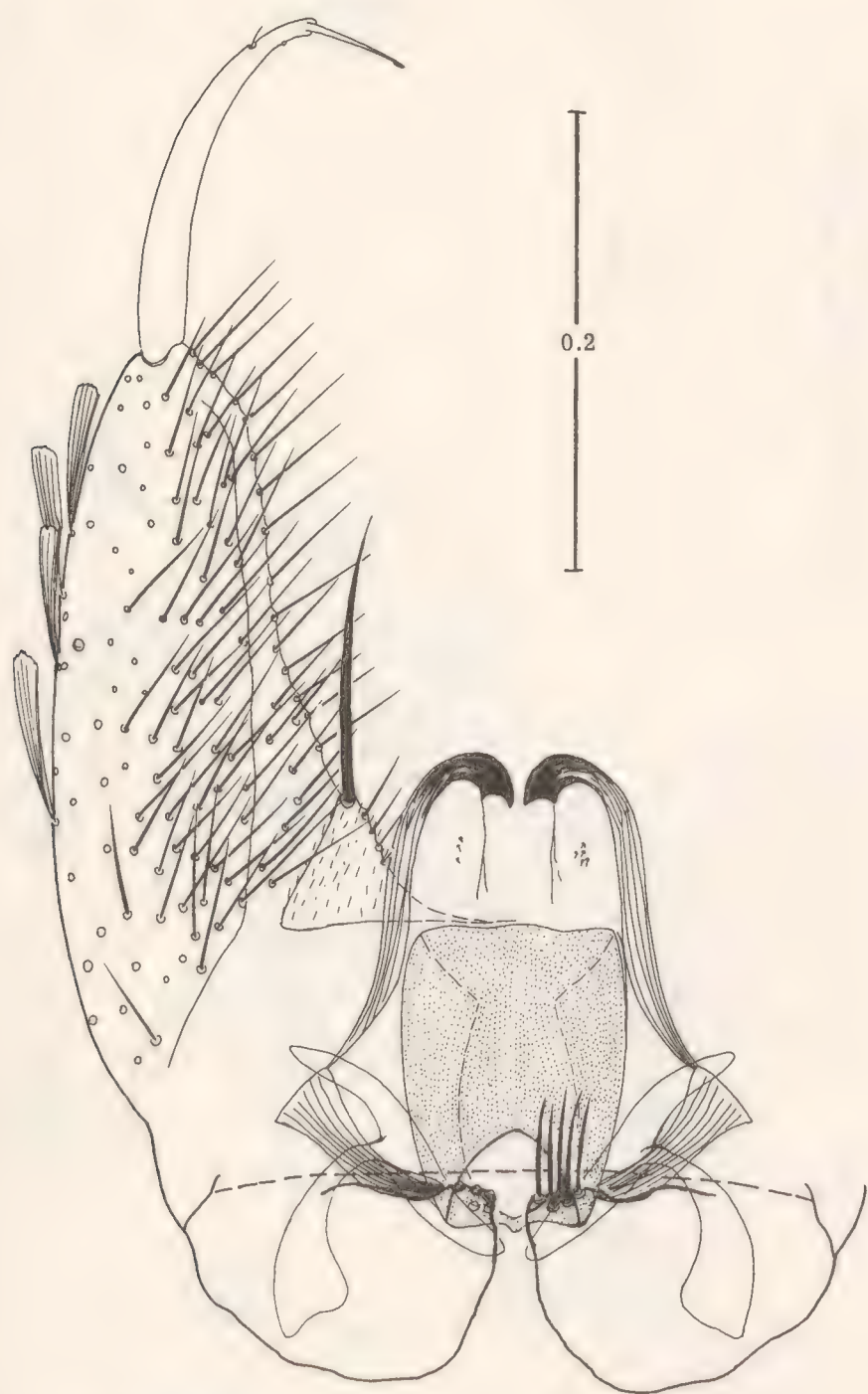
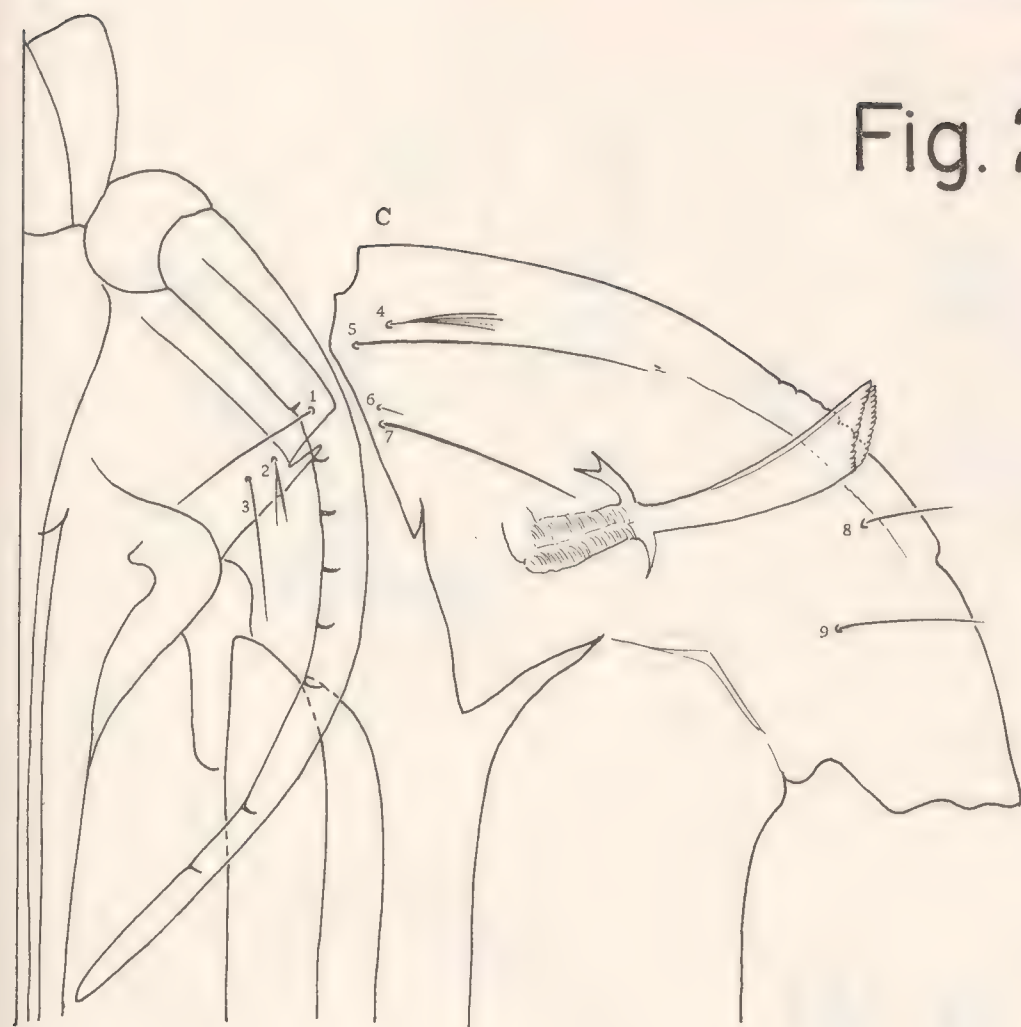
TR 940-111
Arima
St. Andrew
Trinidad

HOWARDINA



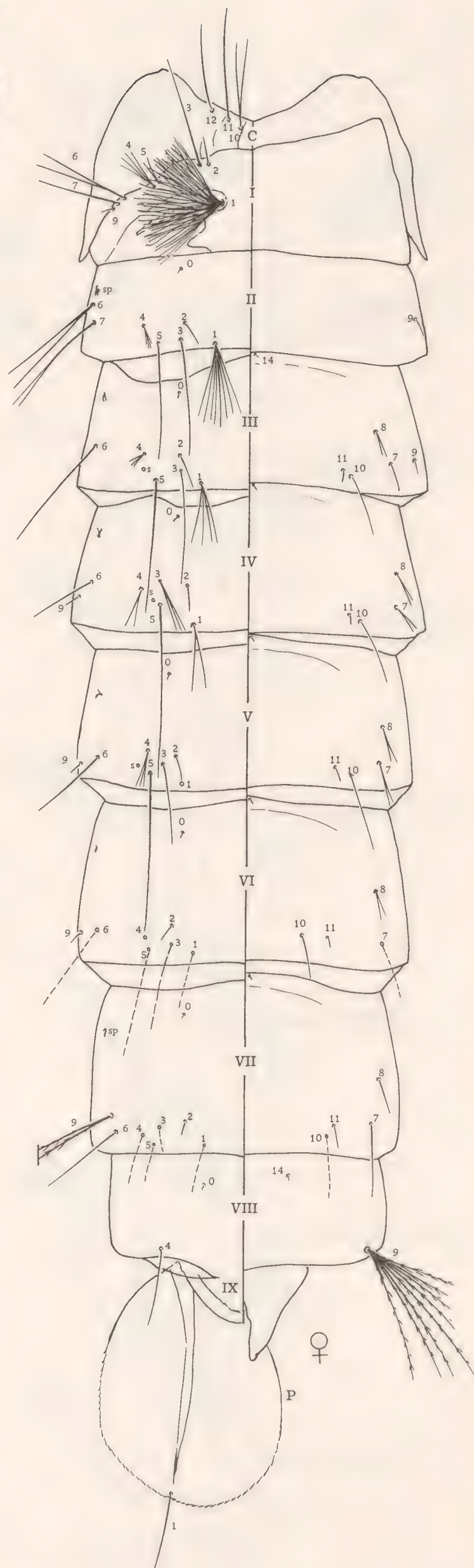
HOWARDINA

Fig. 29



cozumelensis

Island of Cozumel
Yucatan
Mexico



HOWARDINA

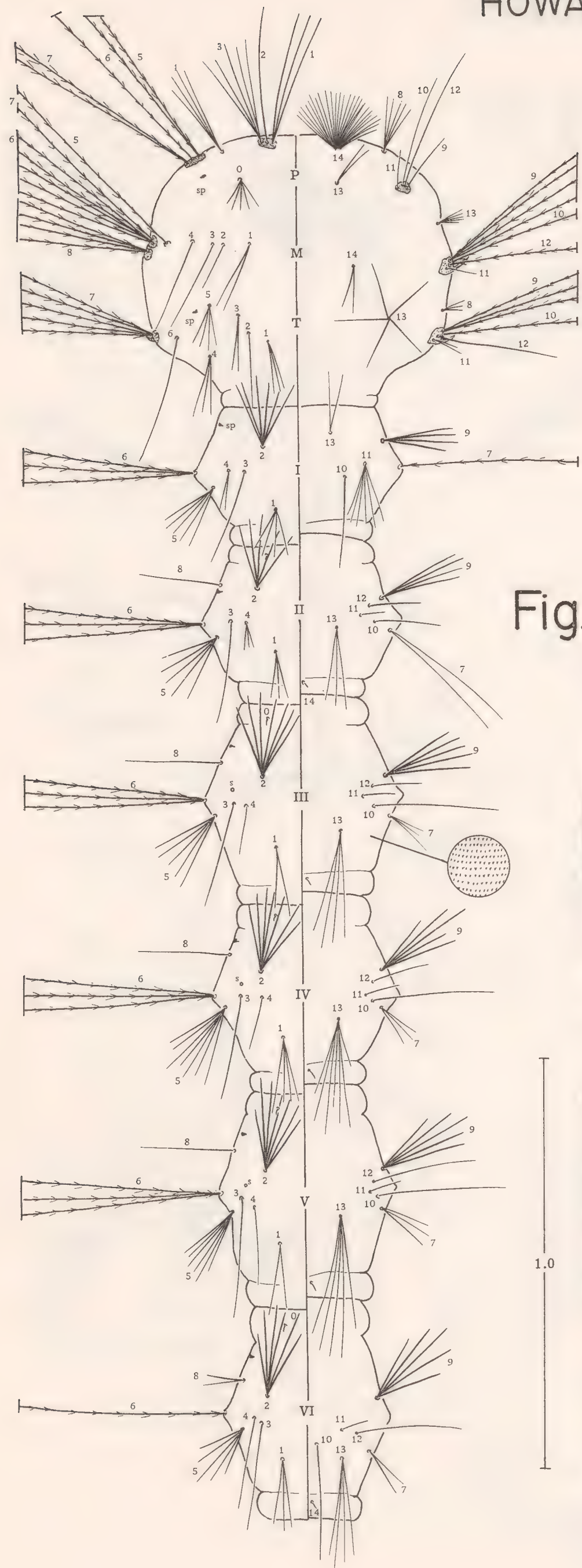
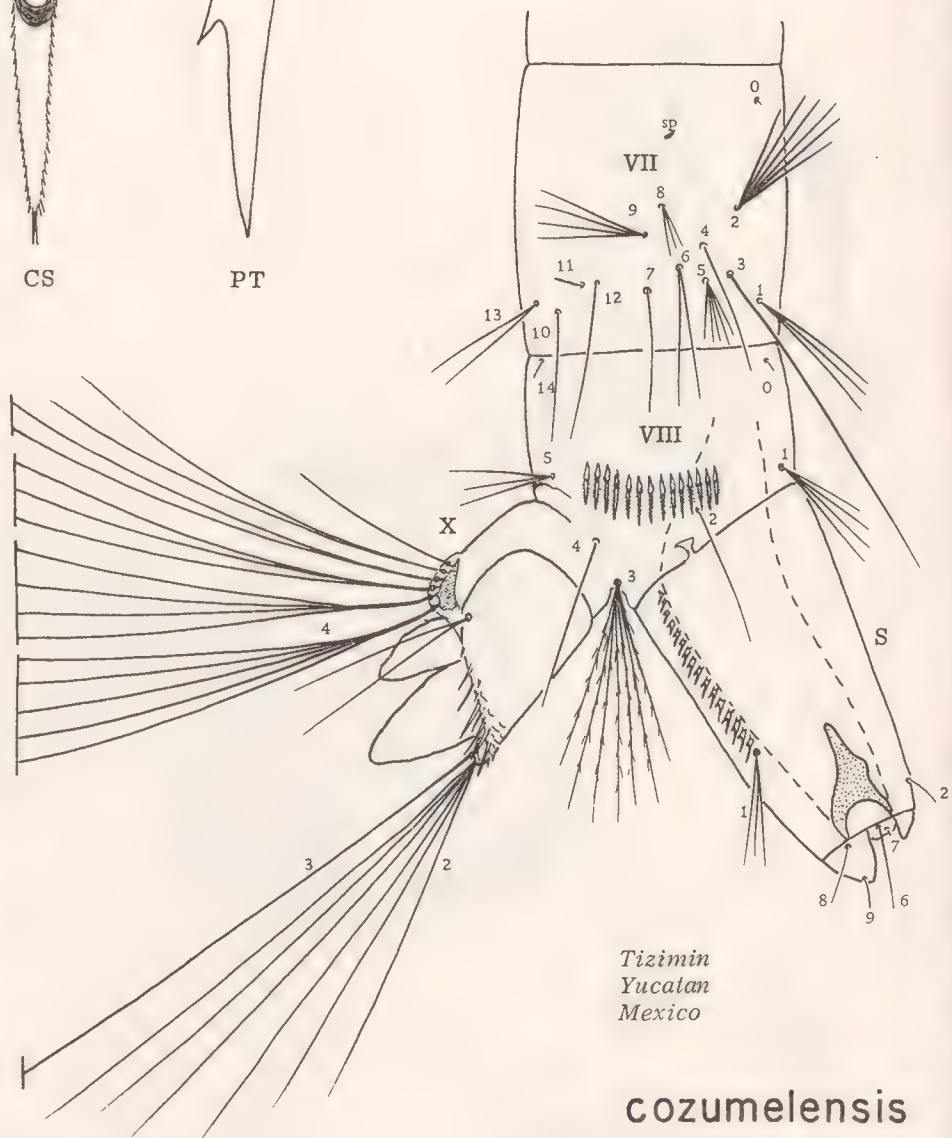
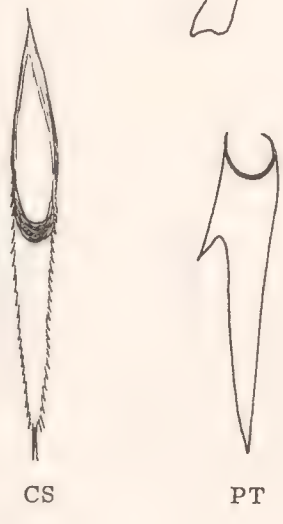
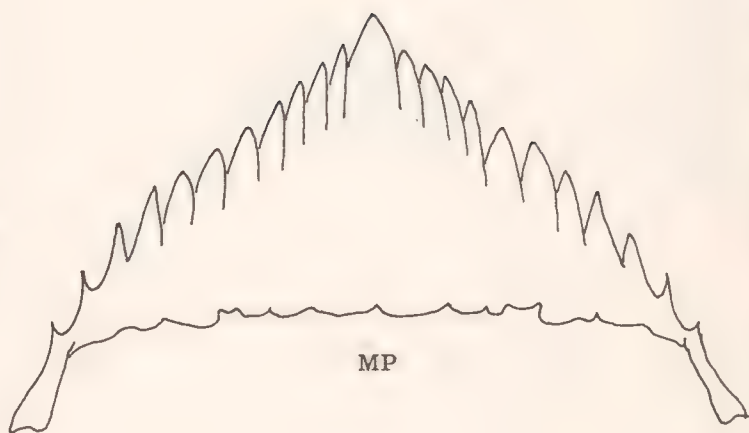
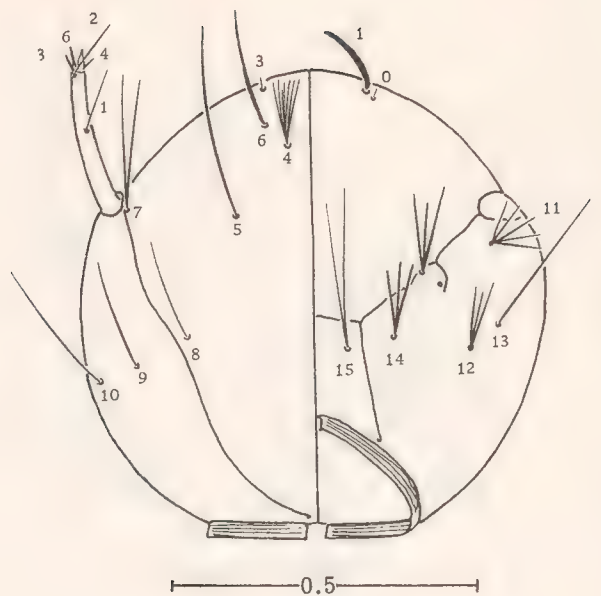


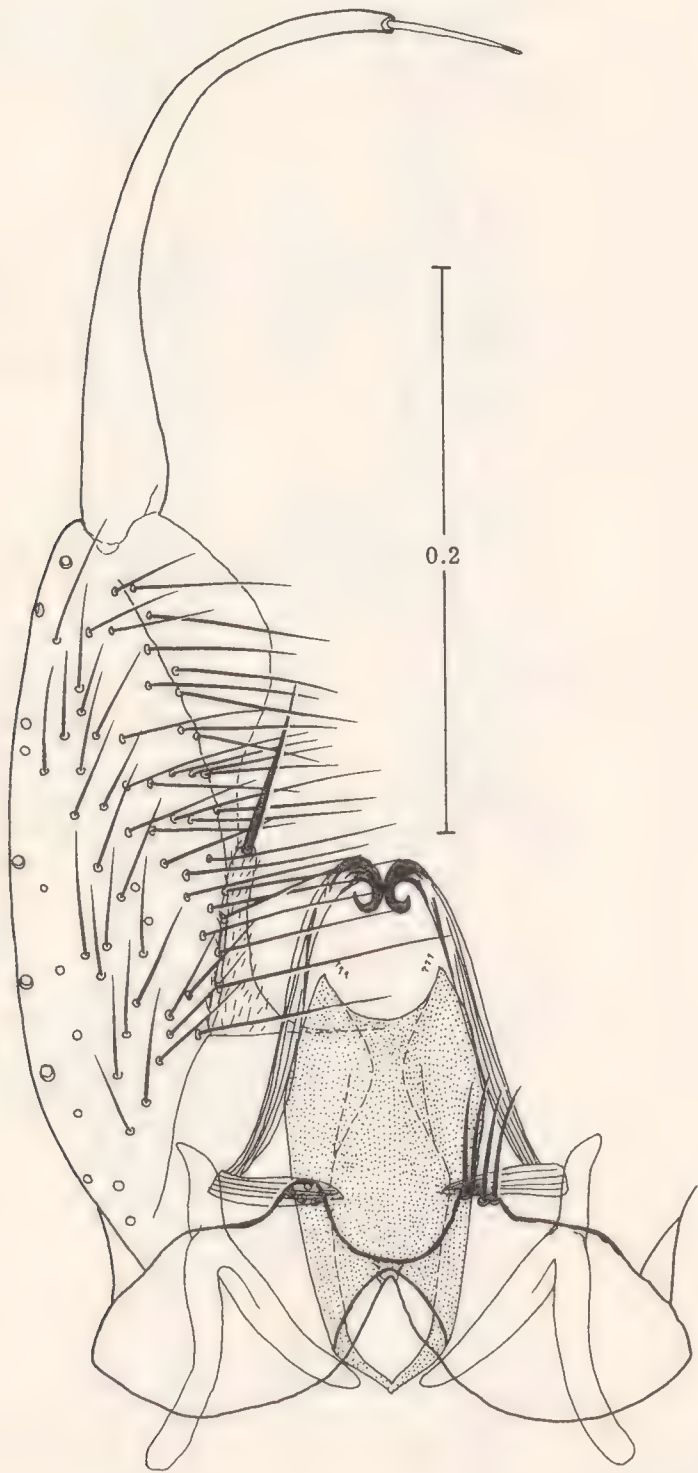
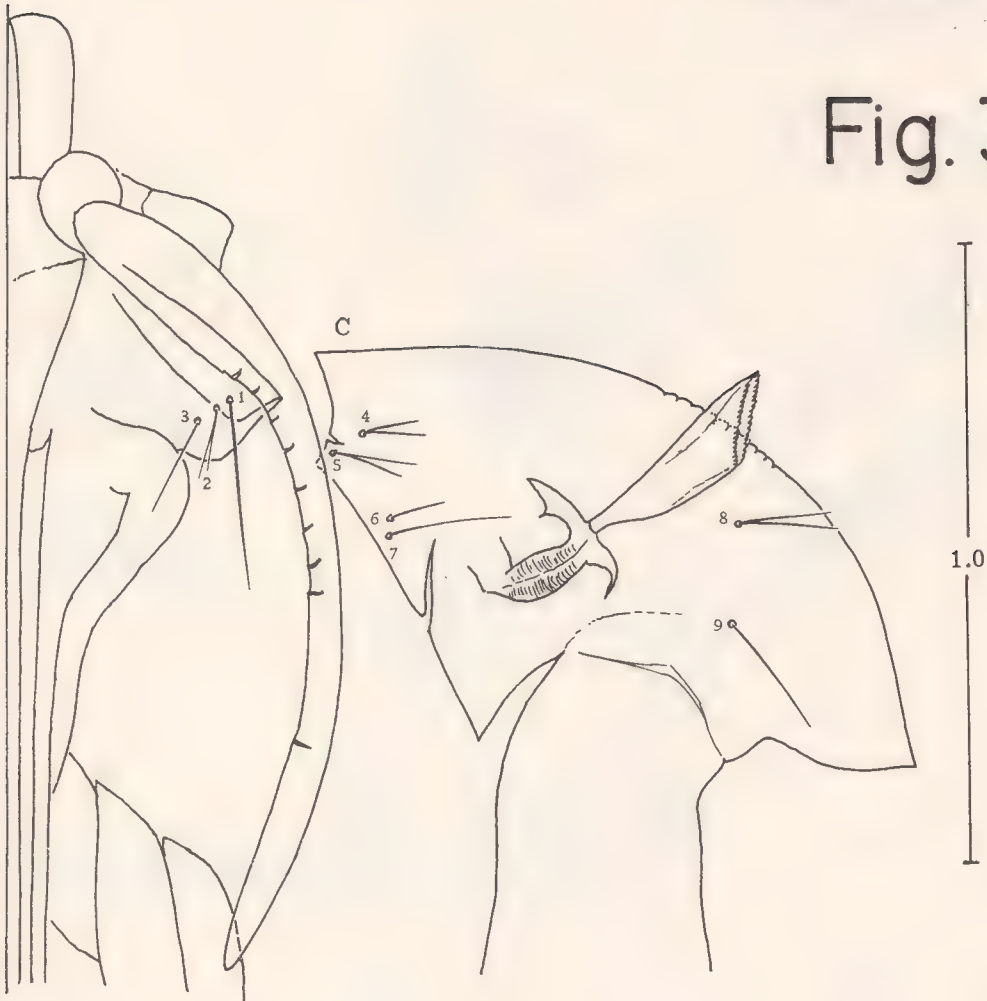
Fig. 30



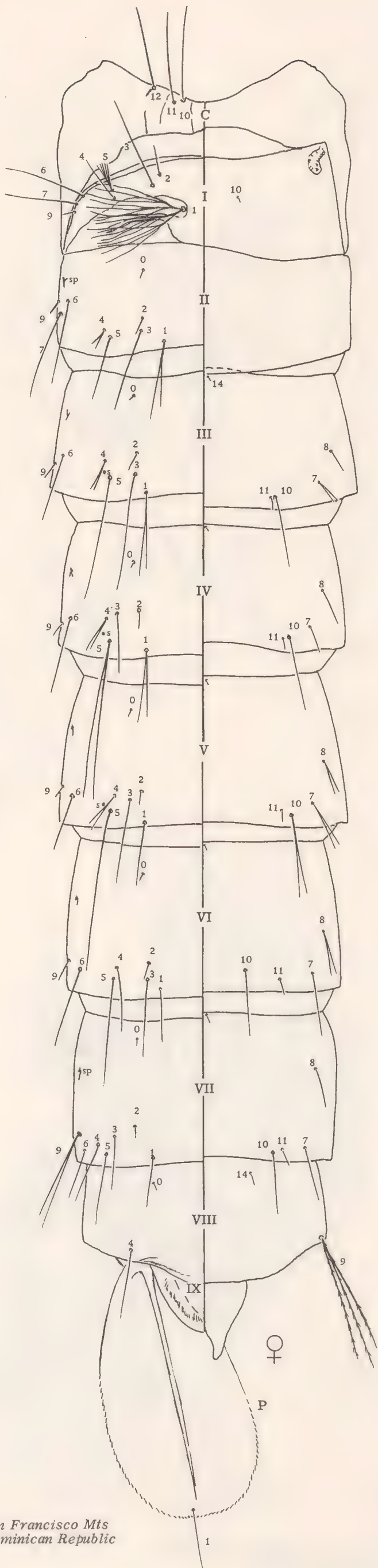
cozumelensis

HOWARDINA

Fig. 31



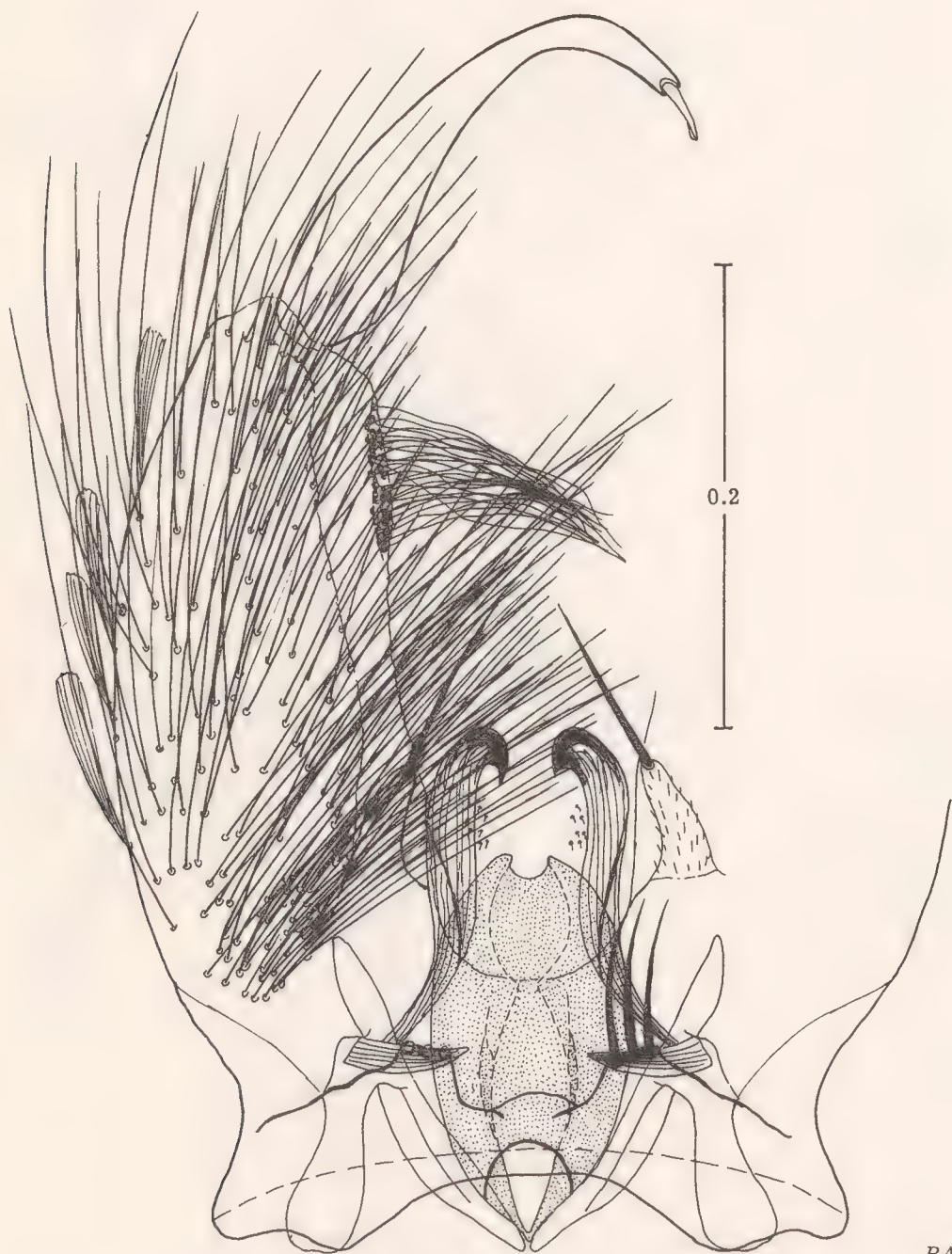
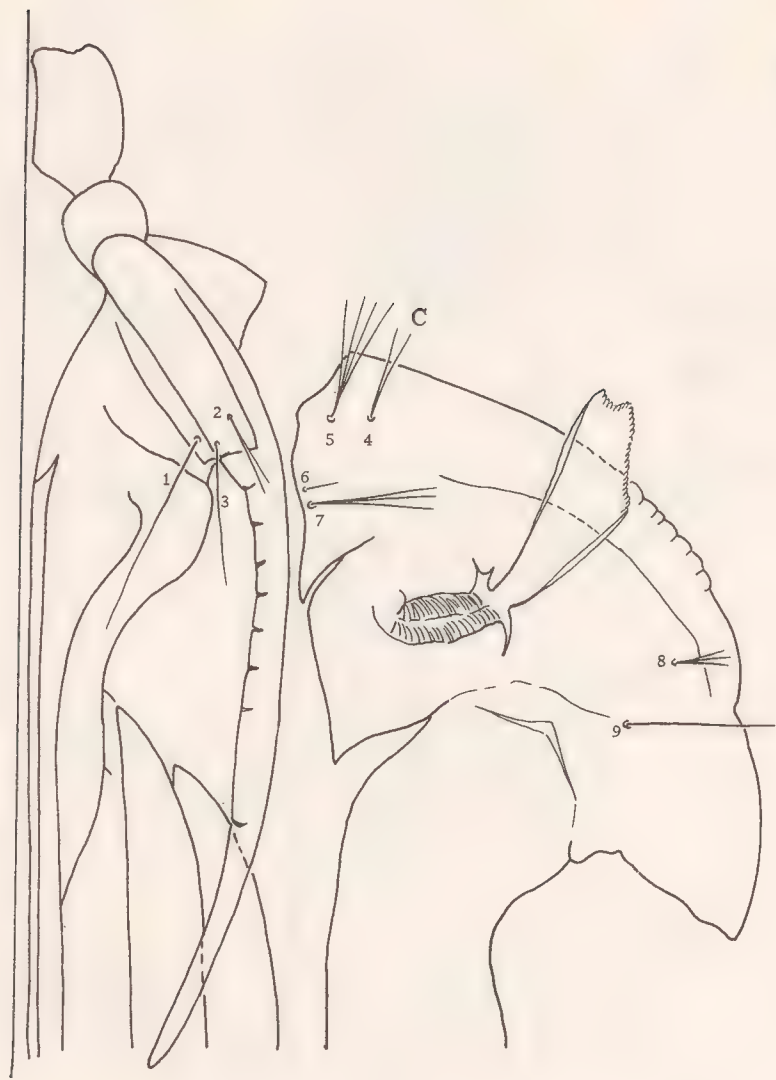
albonotatus



San Francisco Mts
Dominican Republic

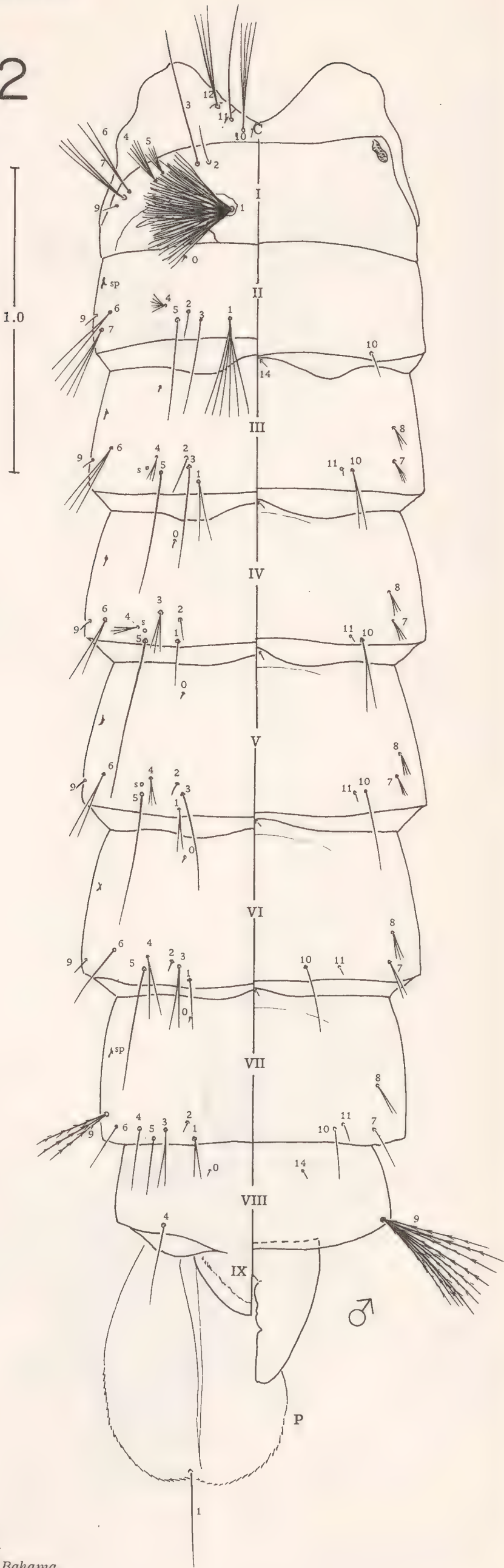
HOWARDINA

Fig. 32



bahamensis

BAH 1
Hunter
Grand Bahama
Bahama Islands



HOWARDINA

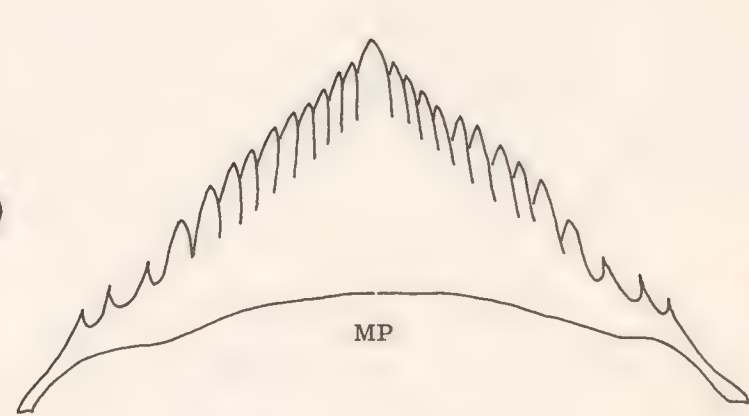
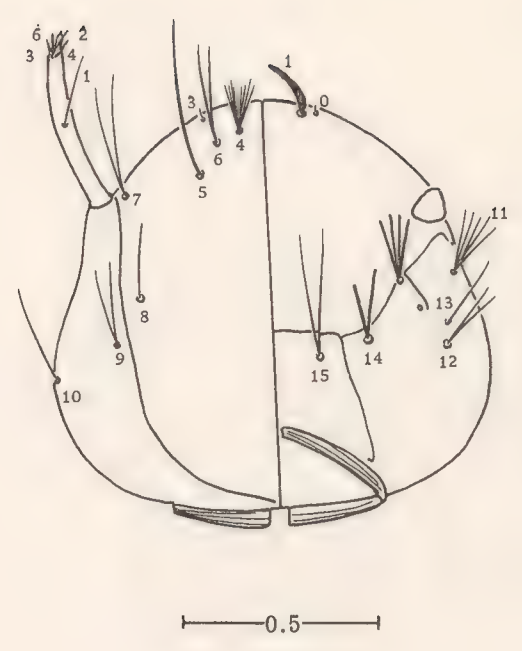
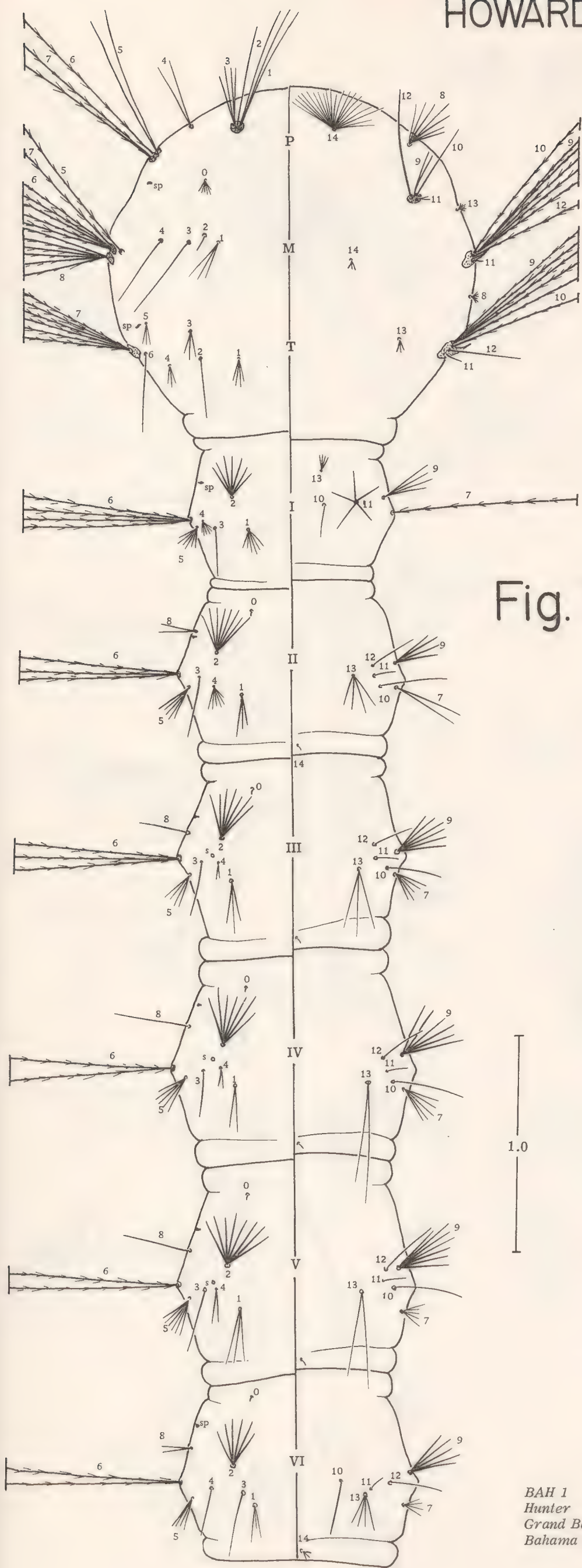
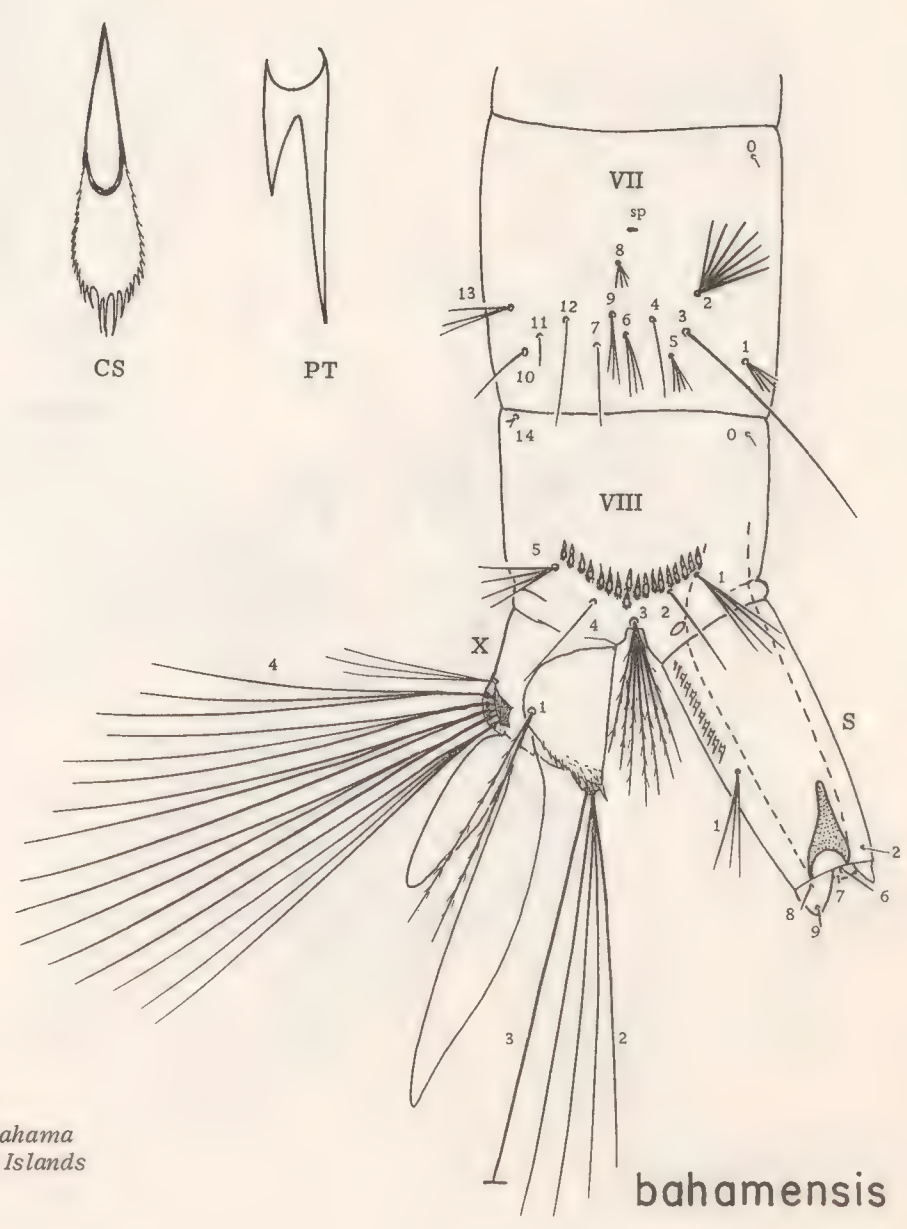


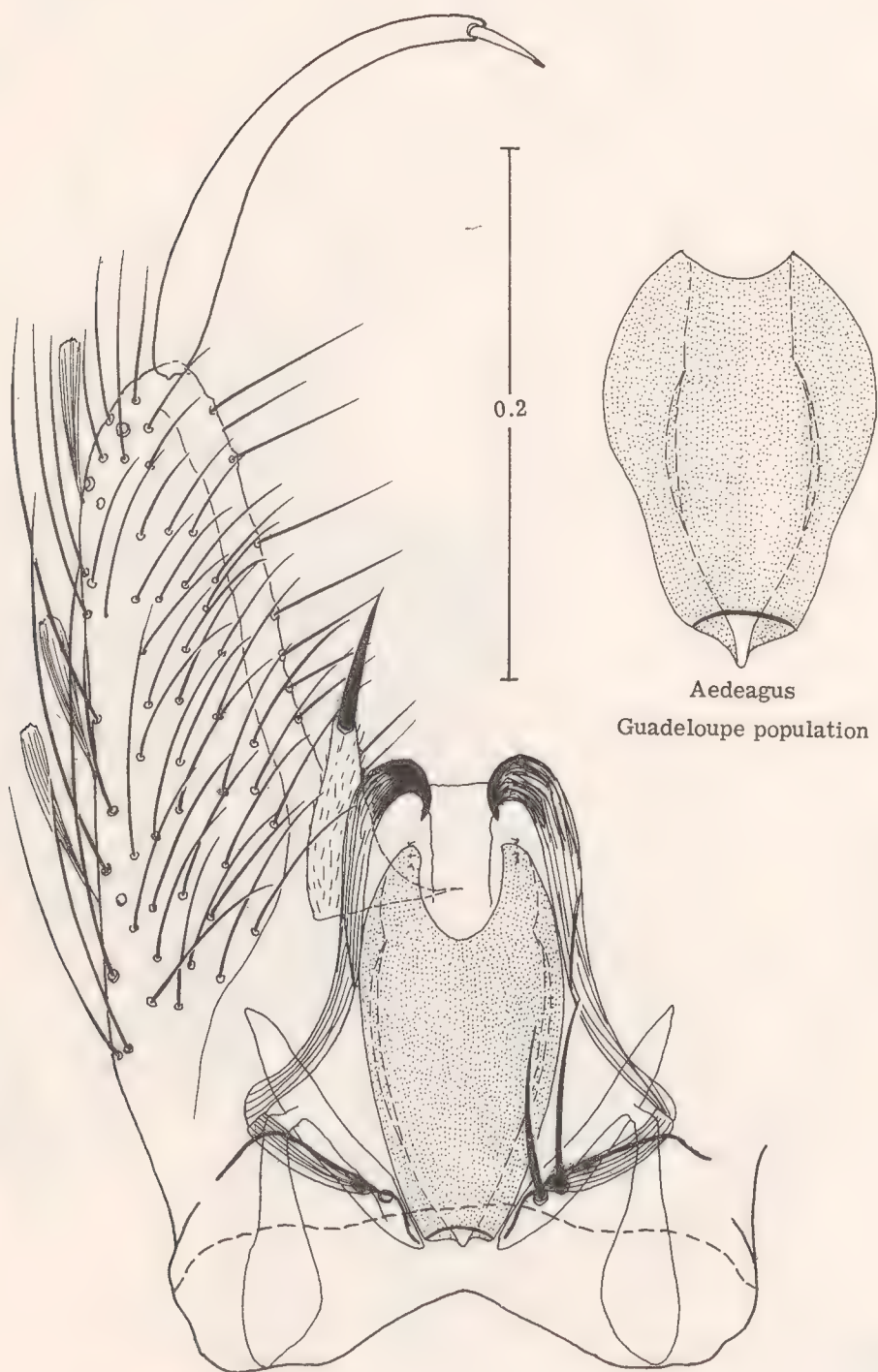
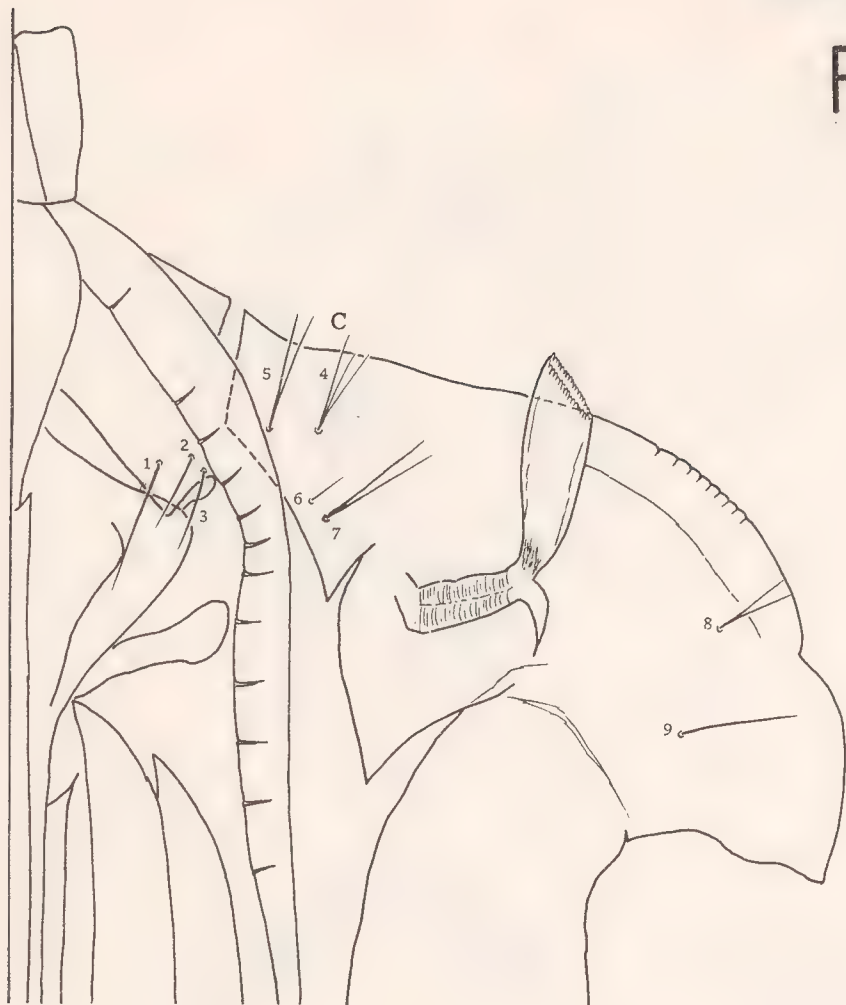
Fig. 33



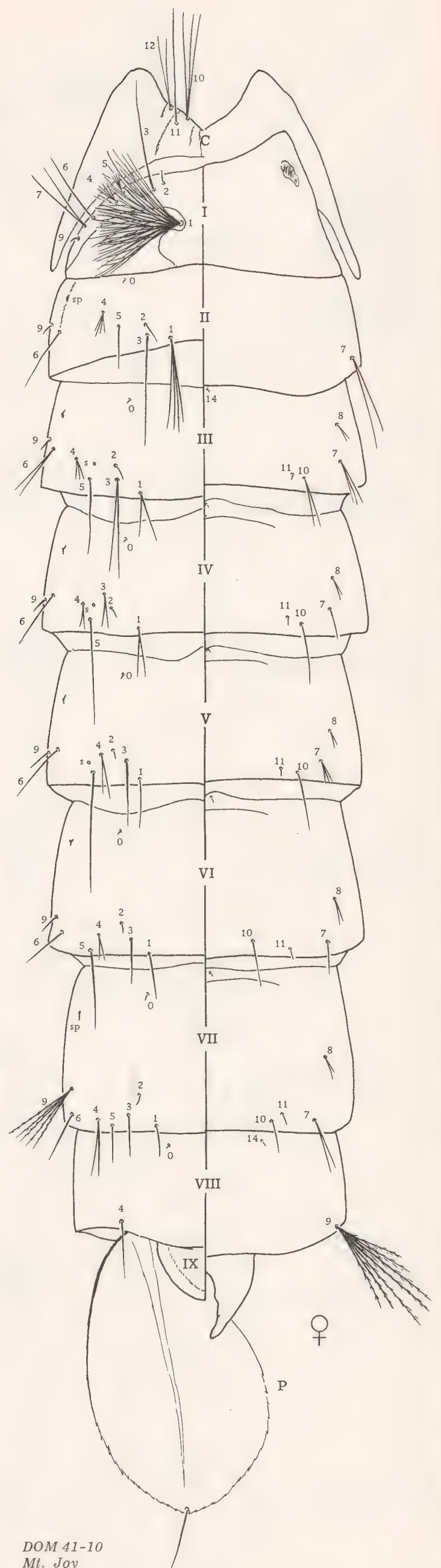
BAH 1
Hunter
Grand Bahama
Bahama Islands

HOWARDINA

Fig. 34



busckii



DOM 41-10
Mt. Joy
St. Paul
Dominica

HOWARDINA

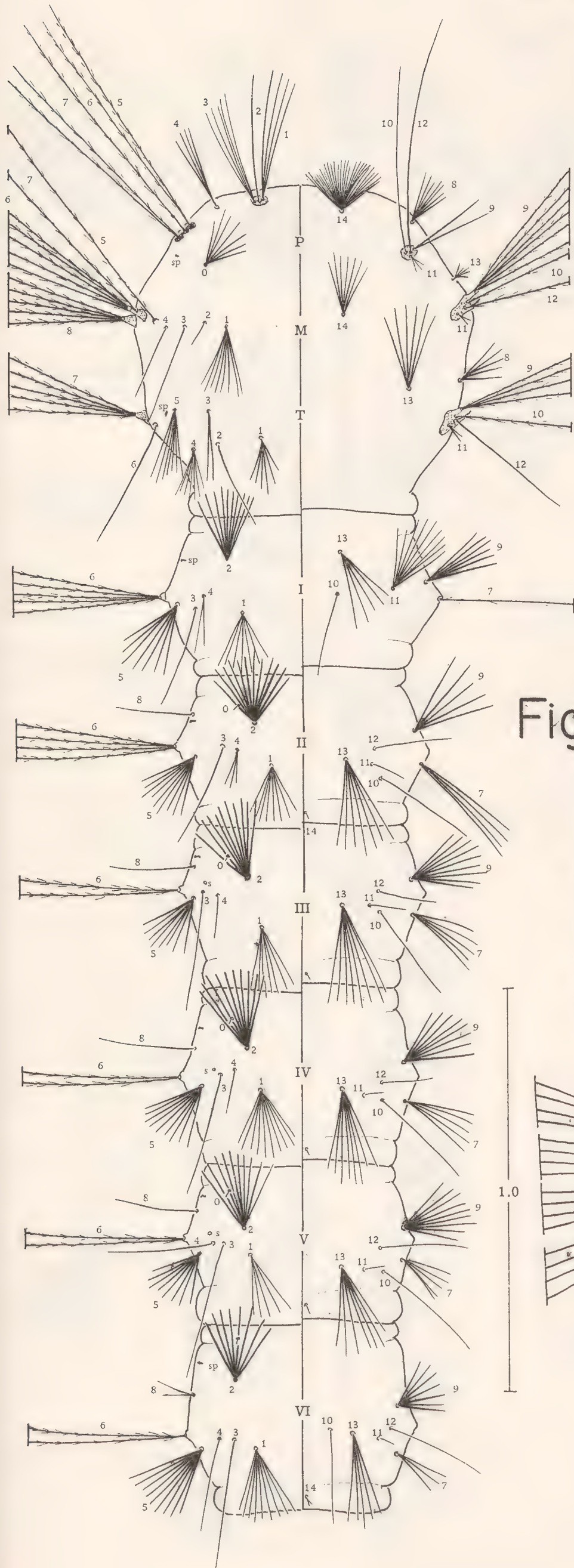
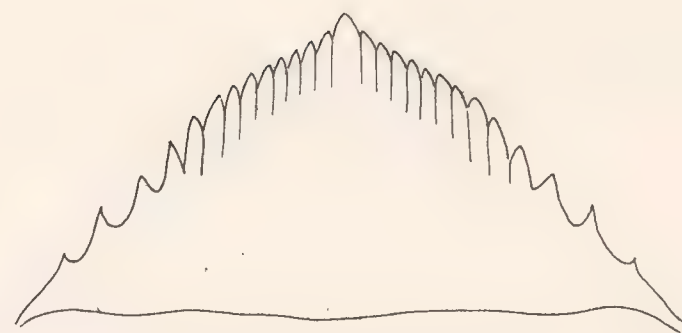
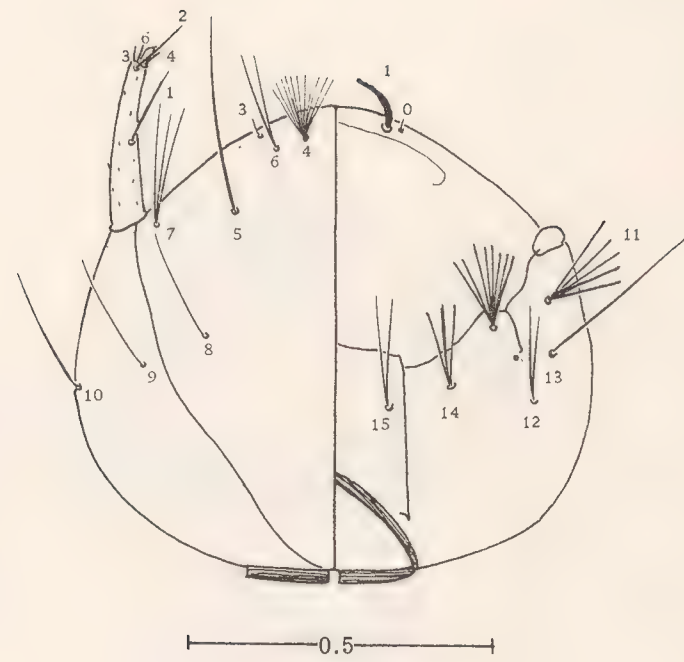
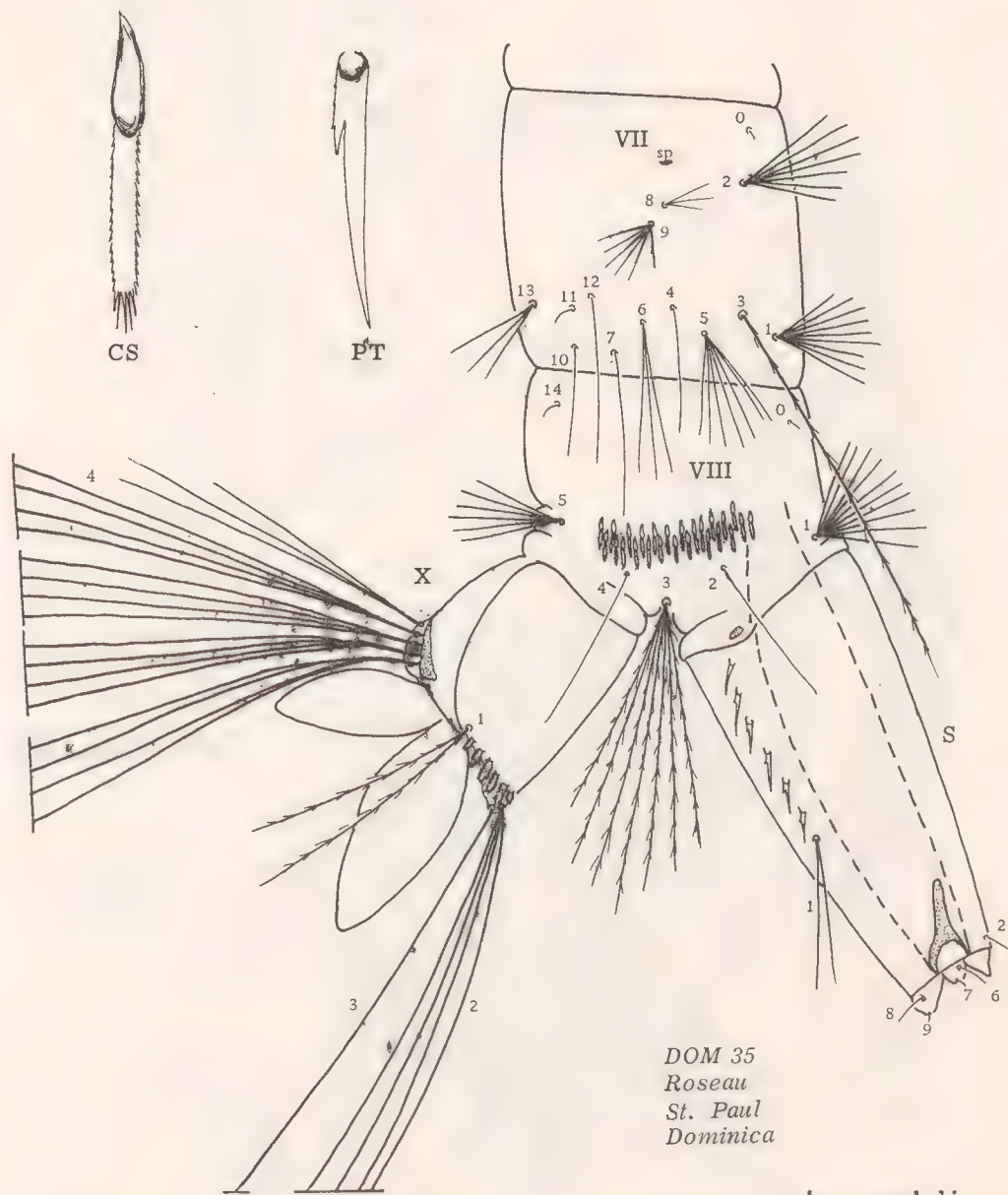


Fig. 35



Mr

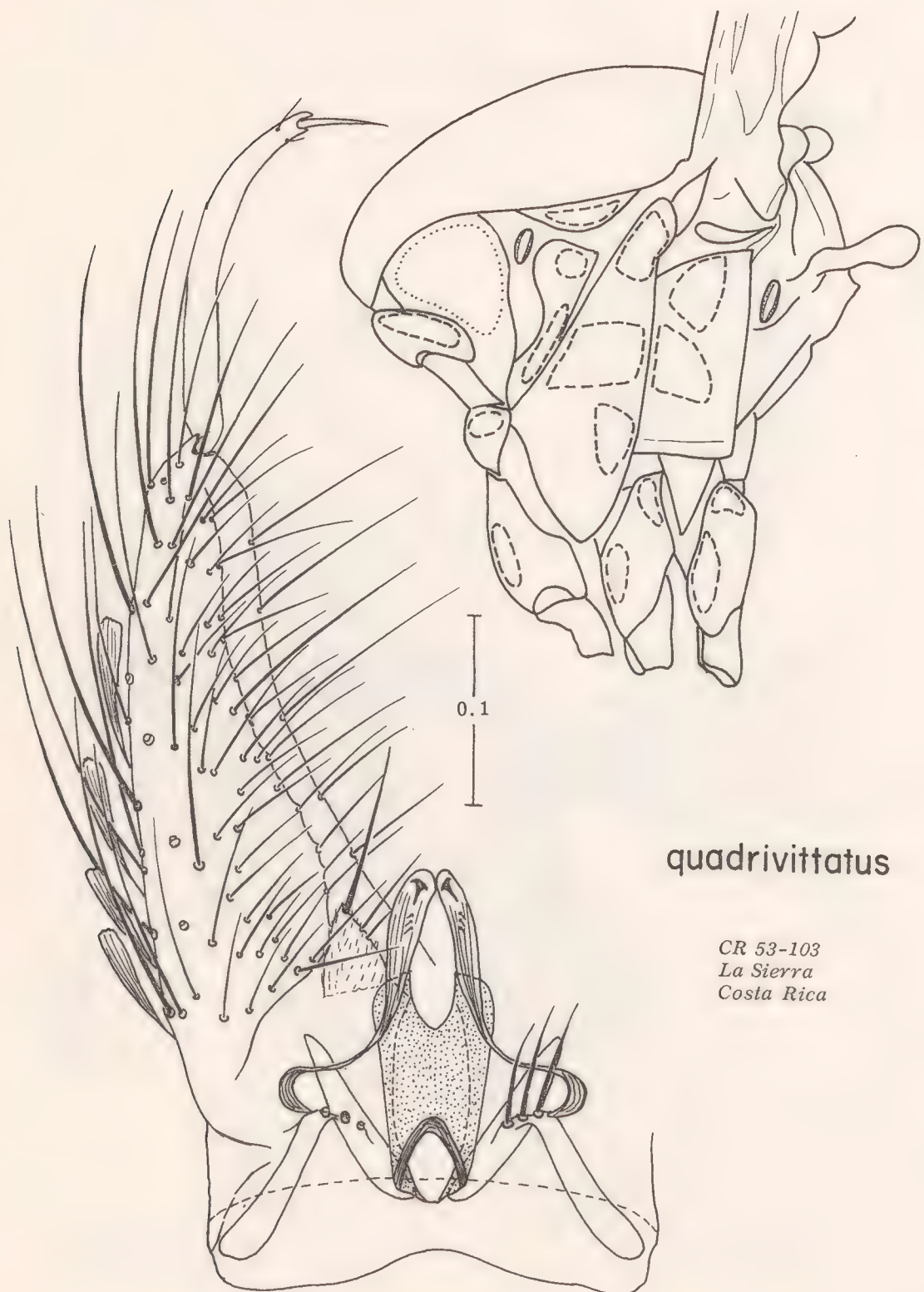
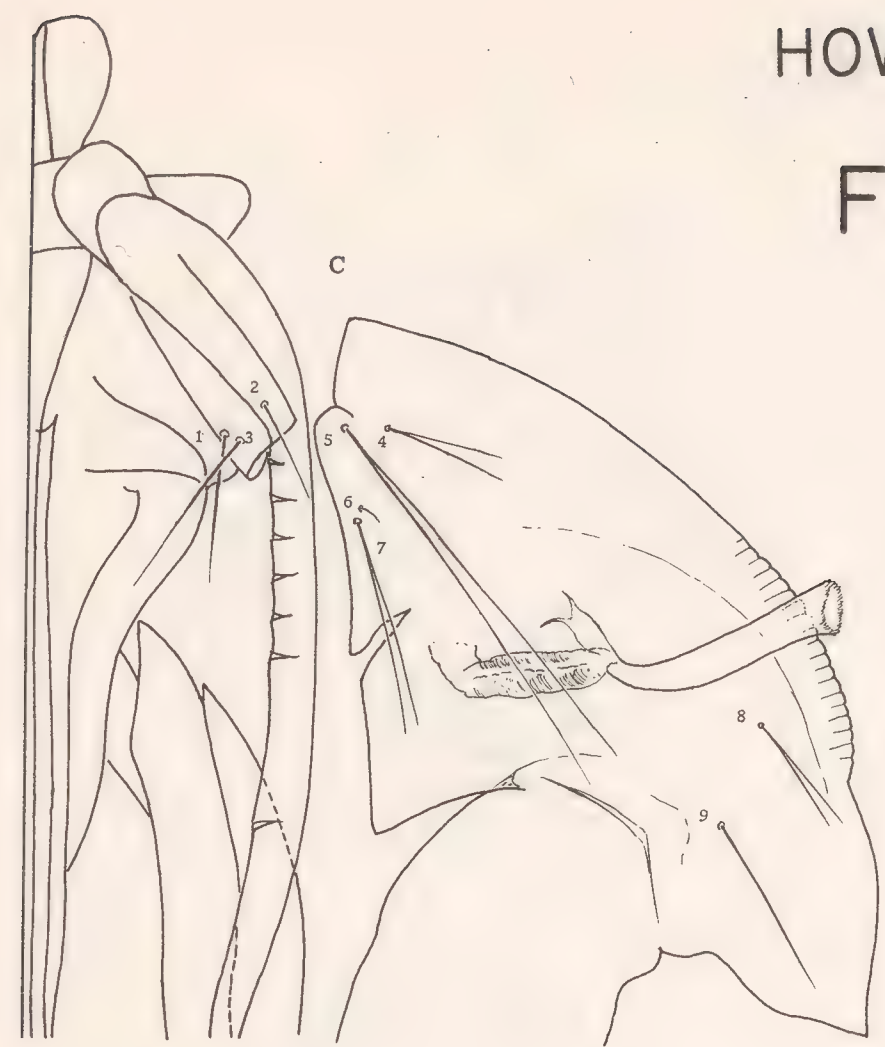


DOM 35
Roseau
St. Paul
Dominica

busckii

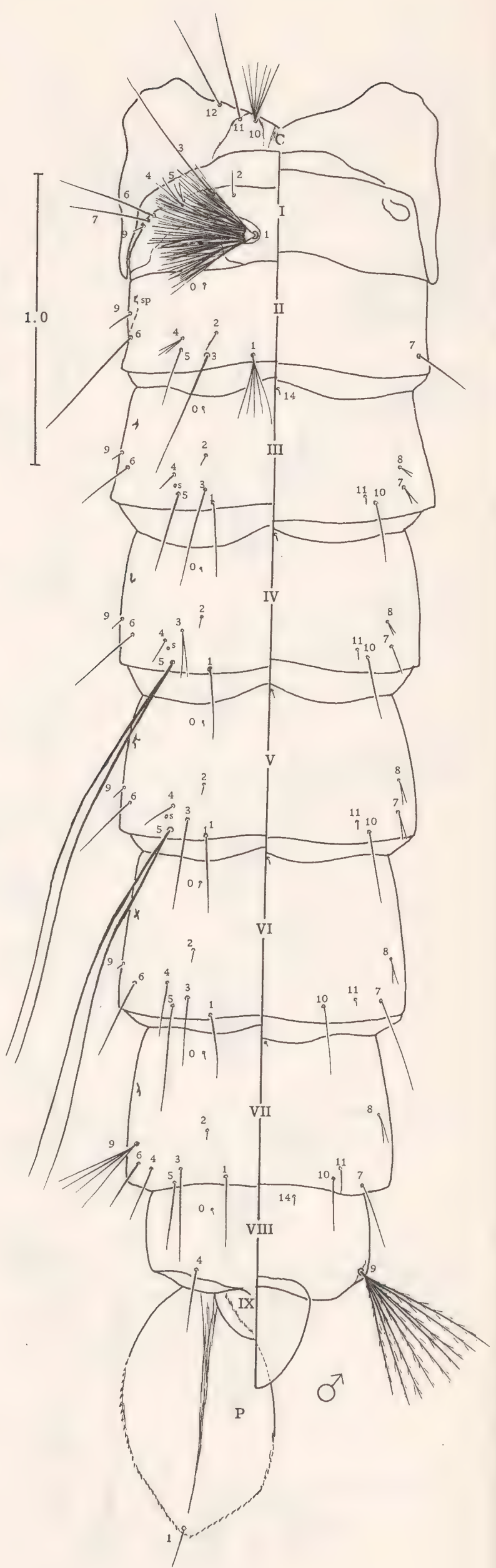
HOWARDINA

Fig. 36



quadrivittatus

CR 53-103
La Sierra
Costa Rica



HOWARDINA

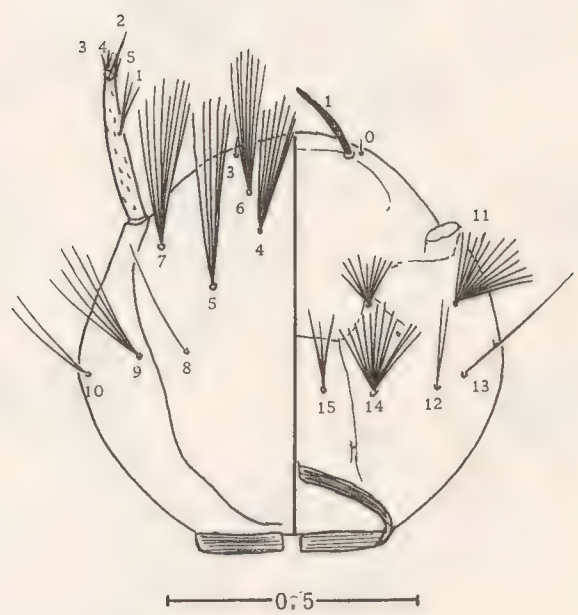
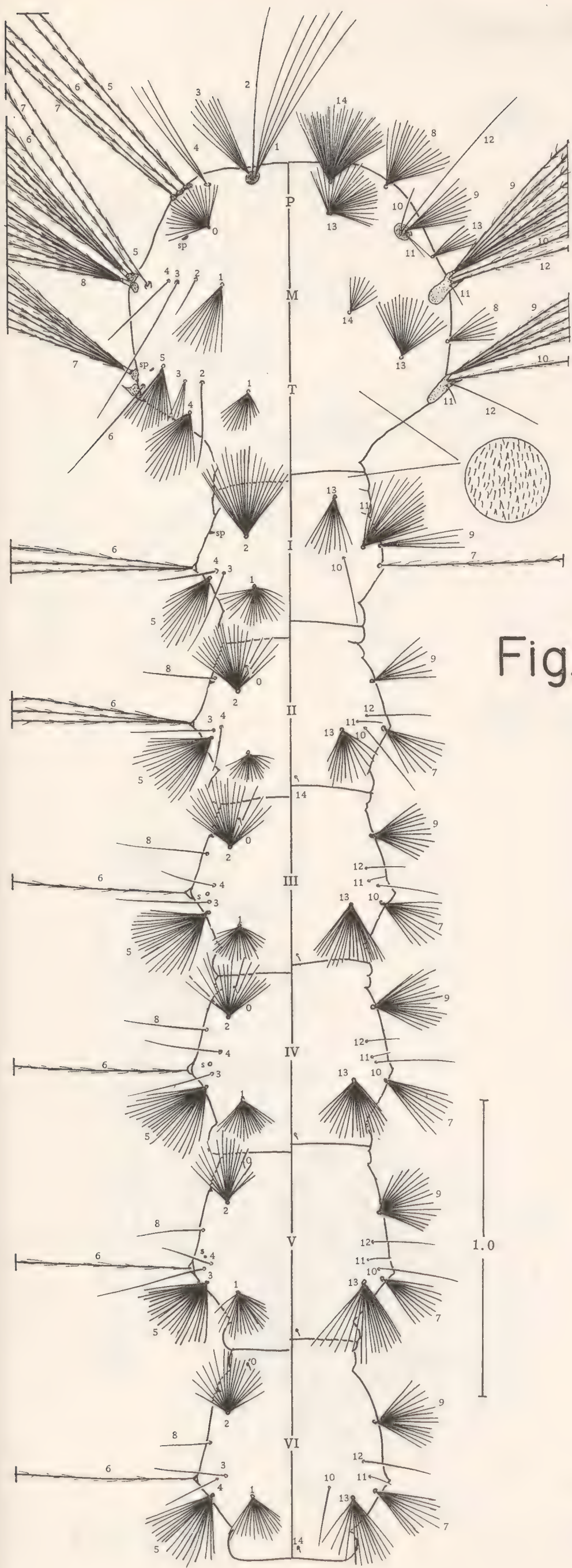
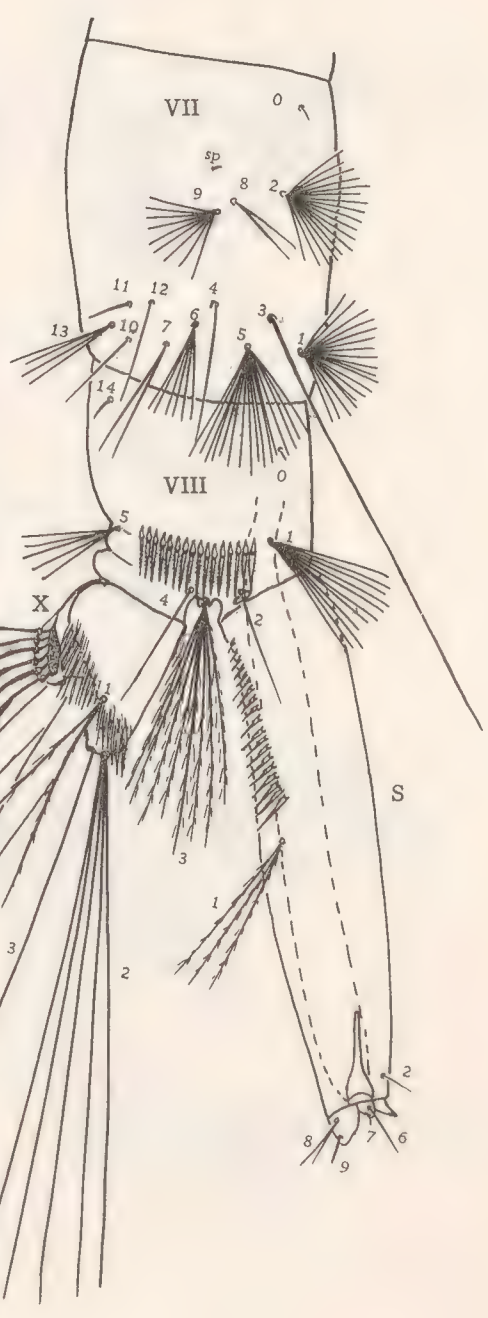


Fig. 37

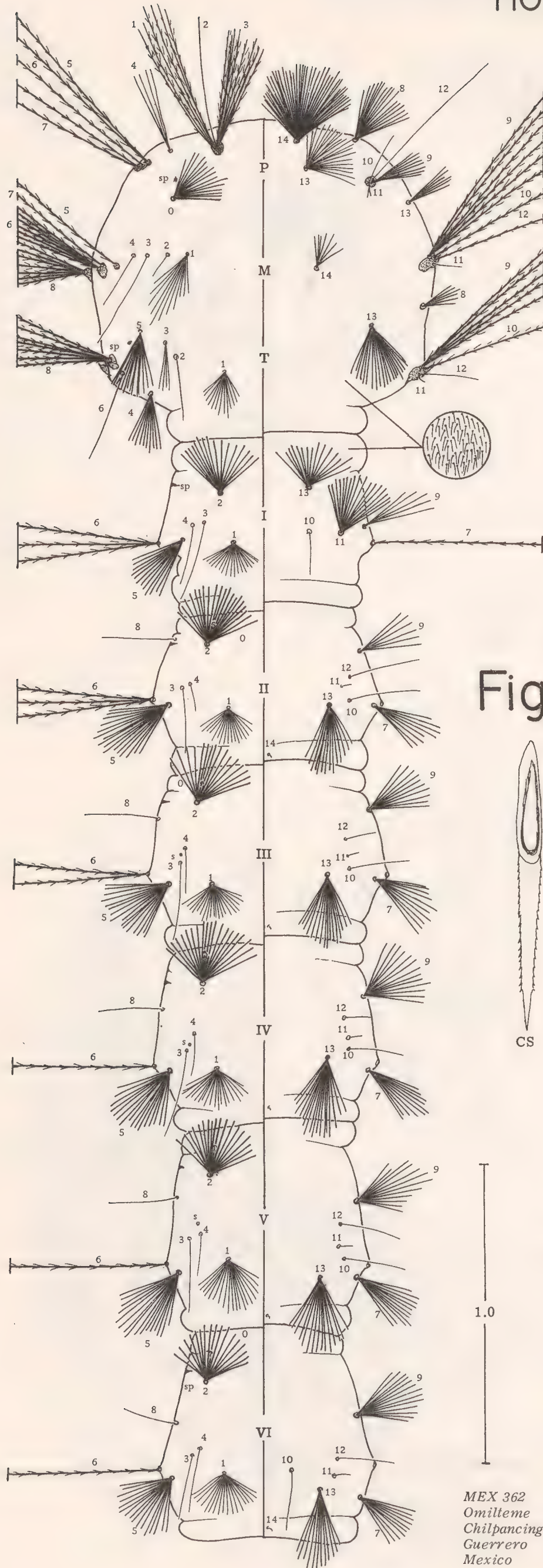


quadrivittatus

CR 51
La Sierra
Costa Rica



HOWARDINA



MEX 362
Omiteme
Chilpancingo
Guerrero
Mexico

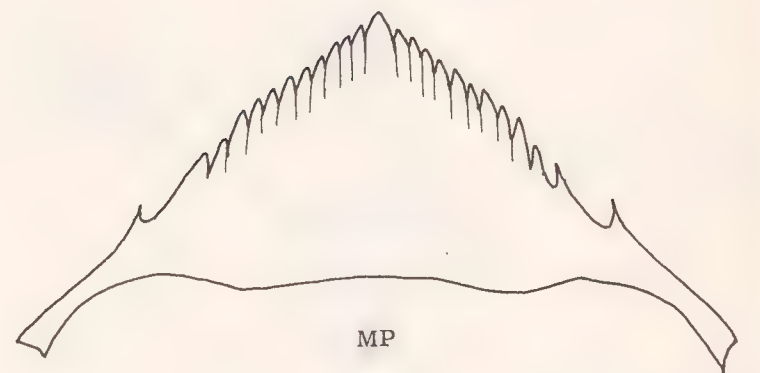
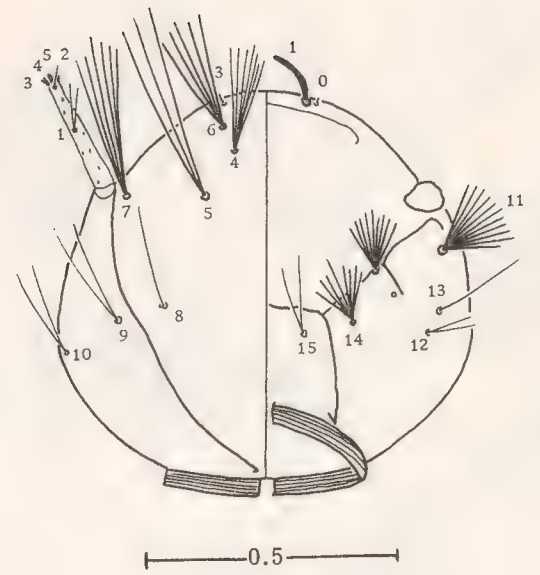
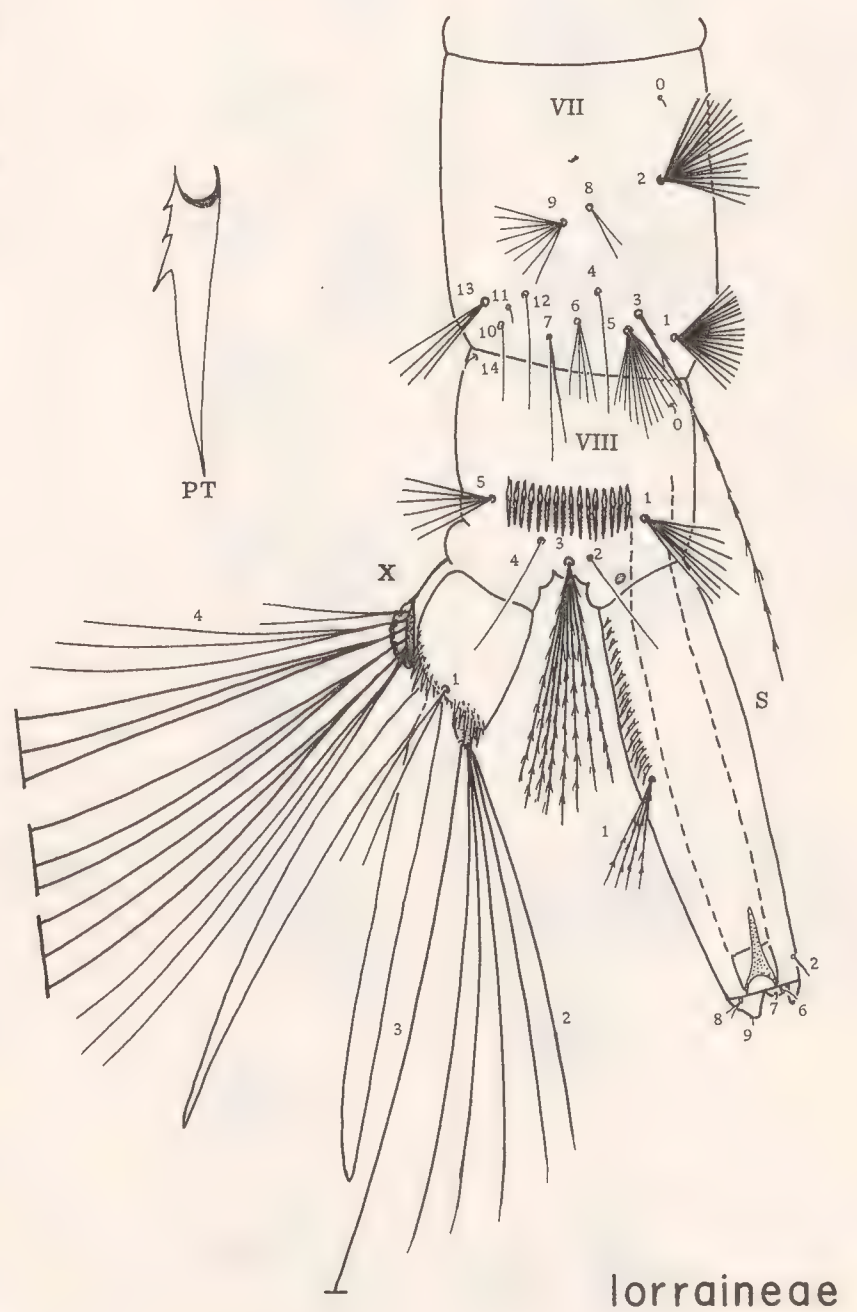


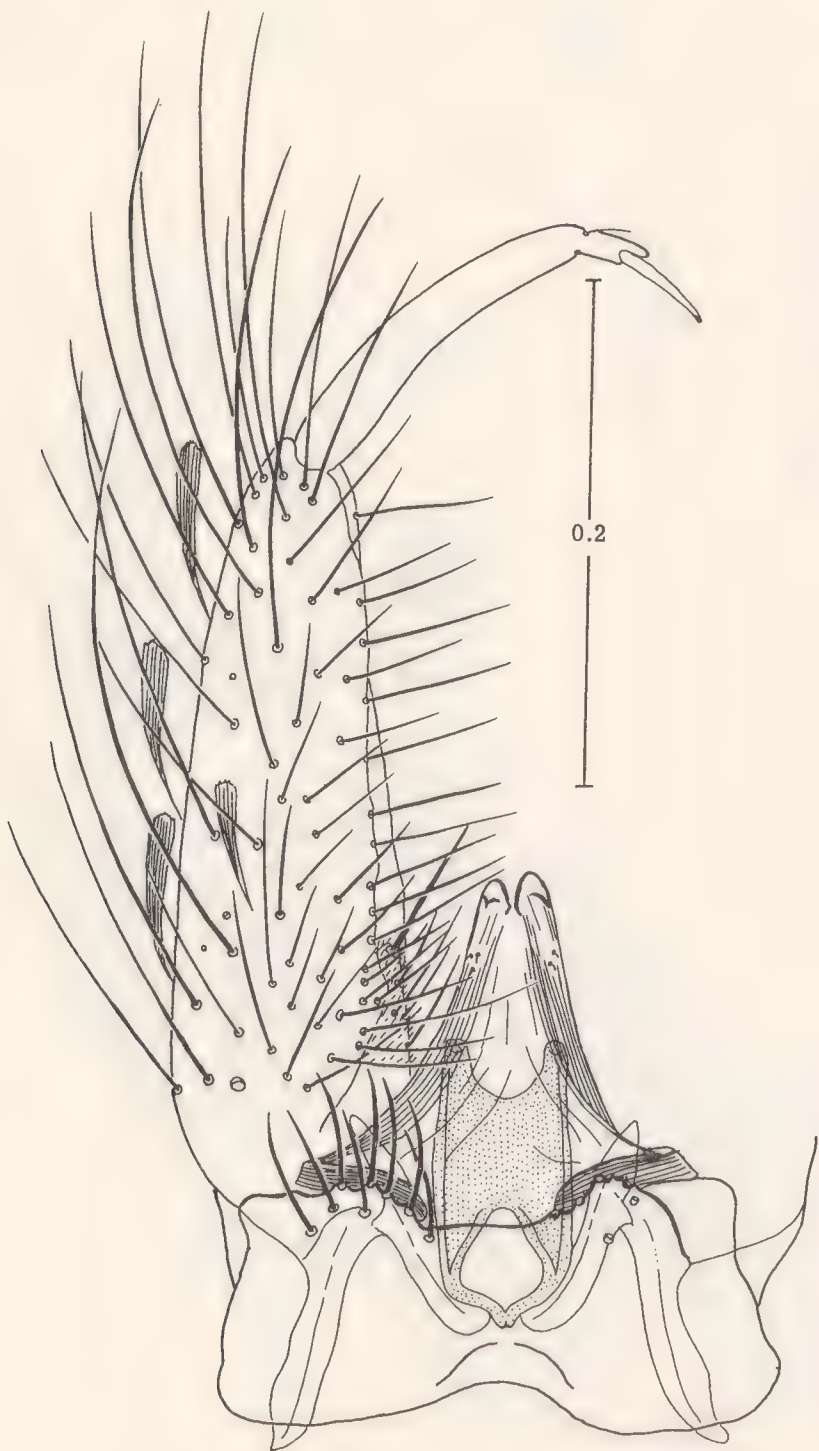
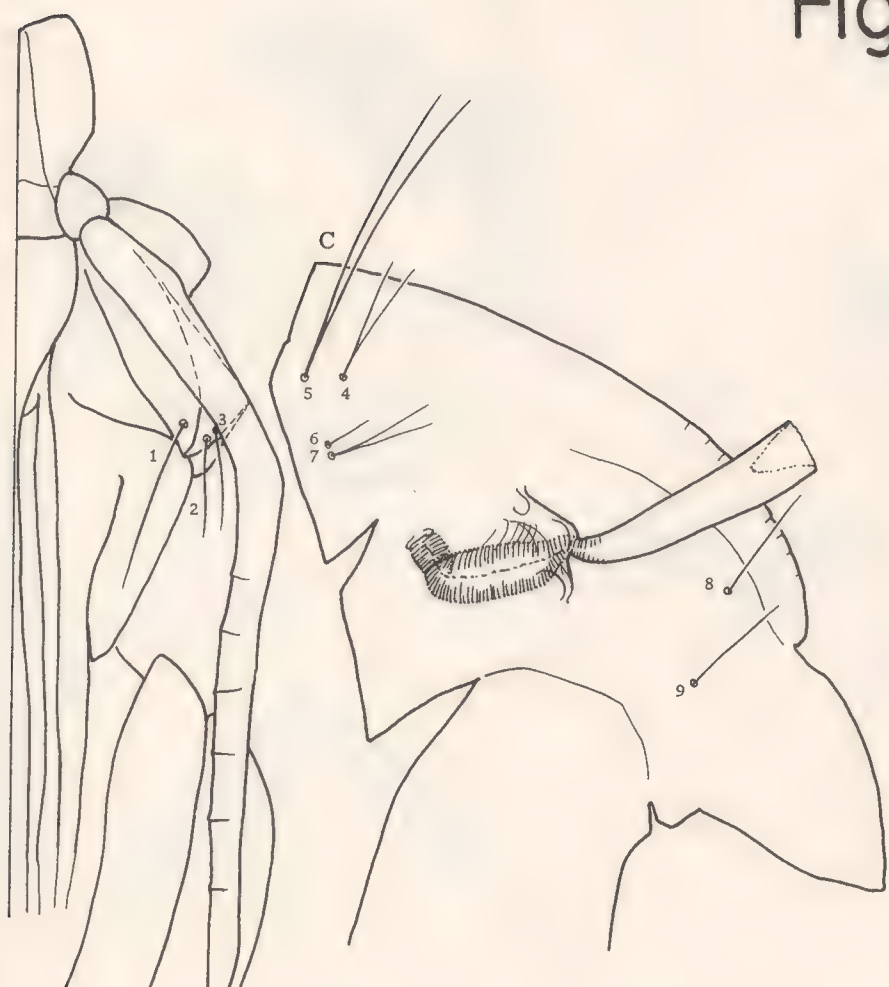
Fig. 38



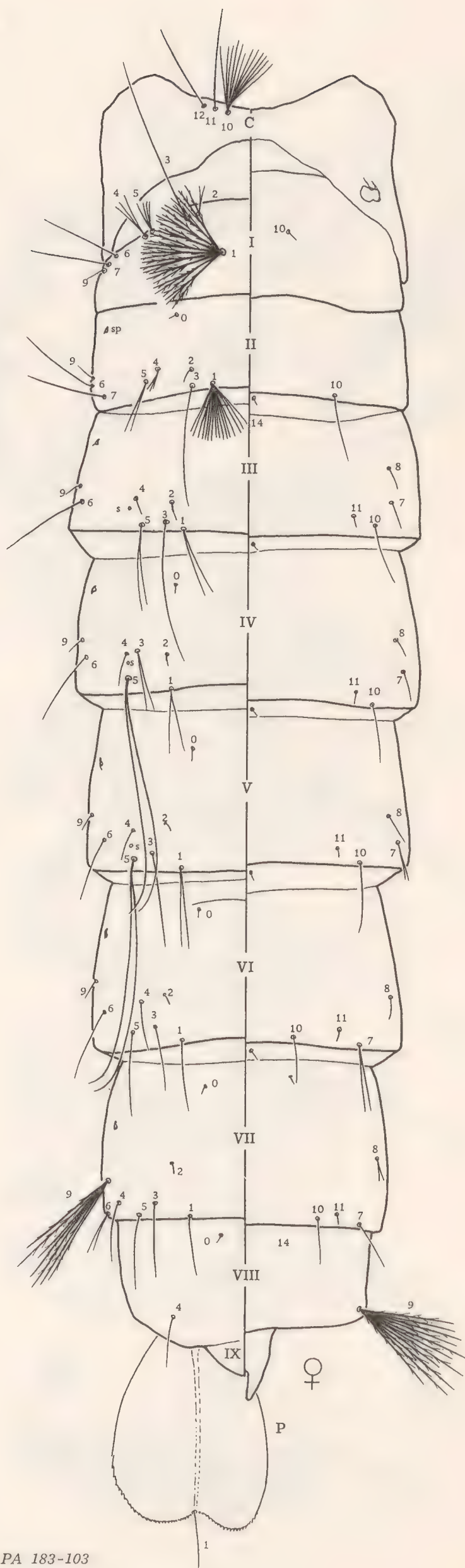
lorraineae

HOWARDINA

Fig. 39

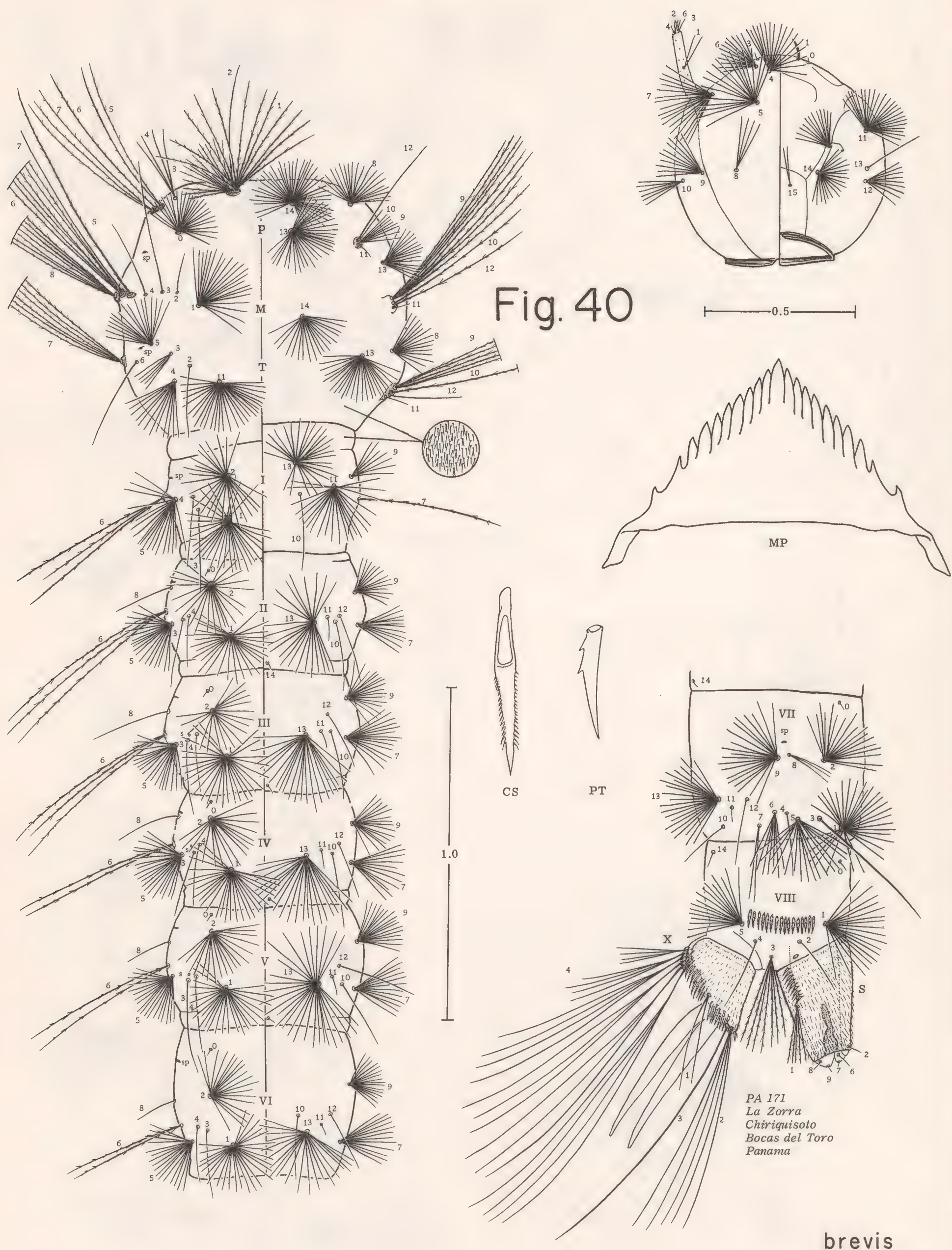


brevis



PA 183-103
La Zorra
Chiriquisito
Bocas del Toro
Panama

HOWARDINA

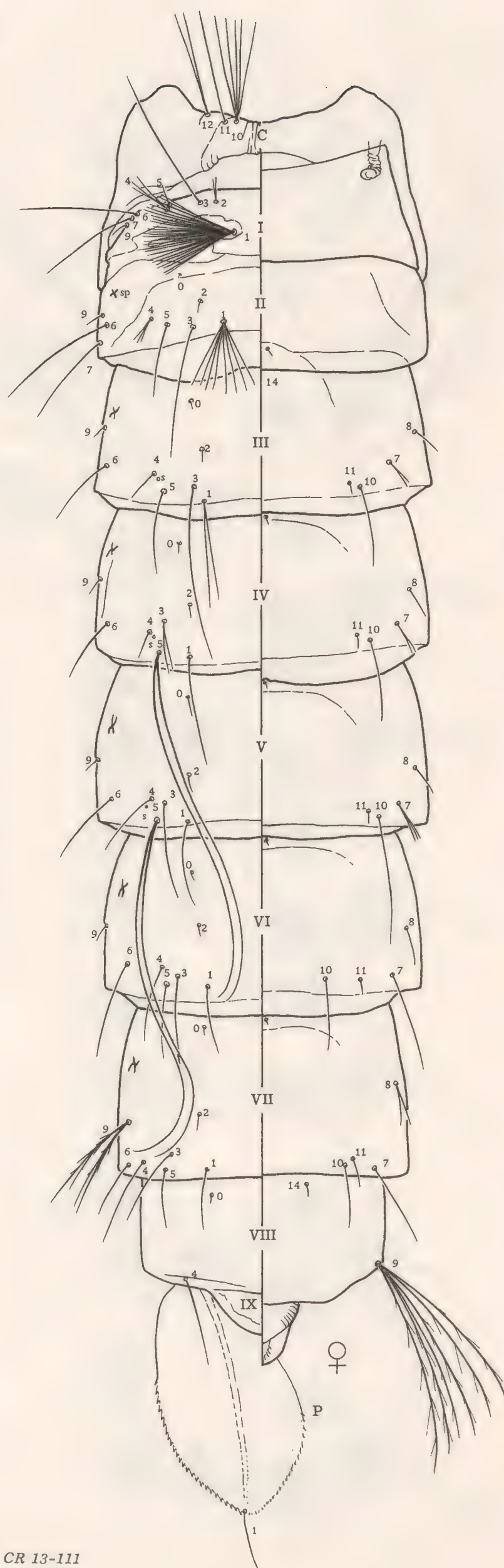


HOWARDINA

Fig. 41



spinosus



CR 13-111
Cervantes
Cartago
Costa Rica

HOWARDINA

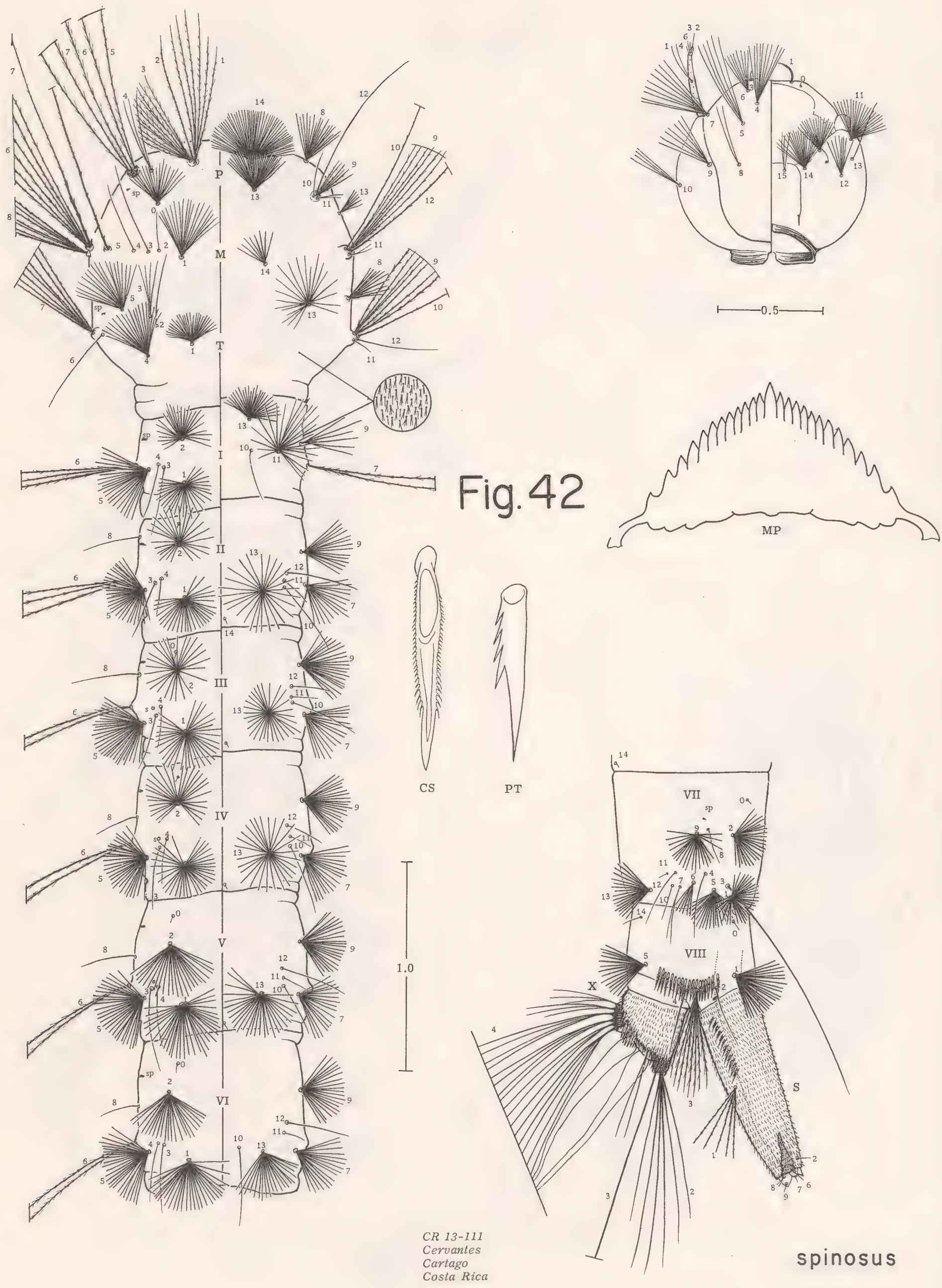
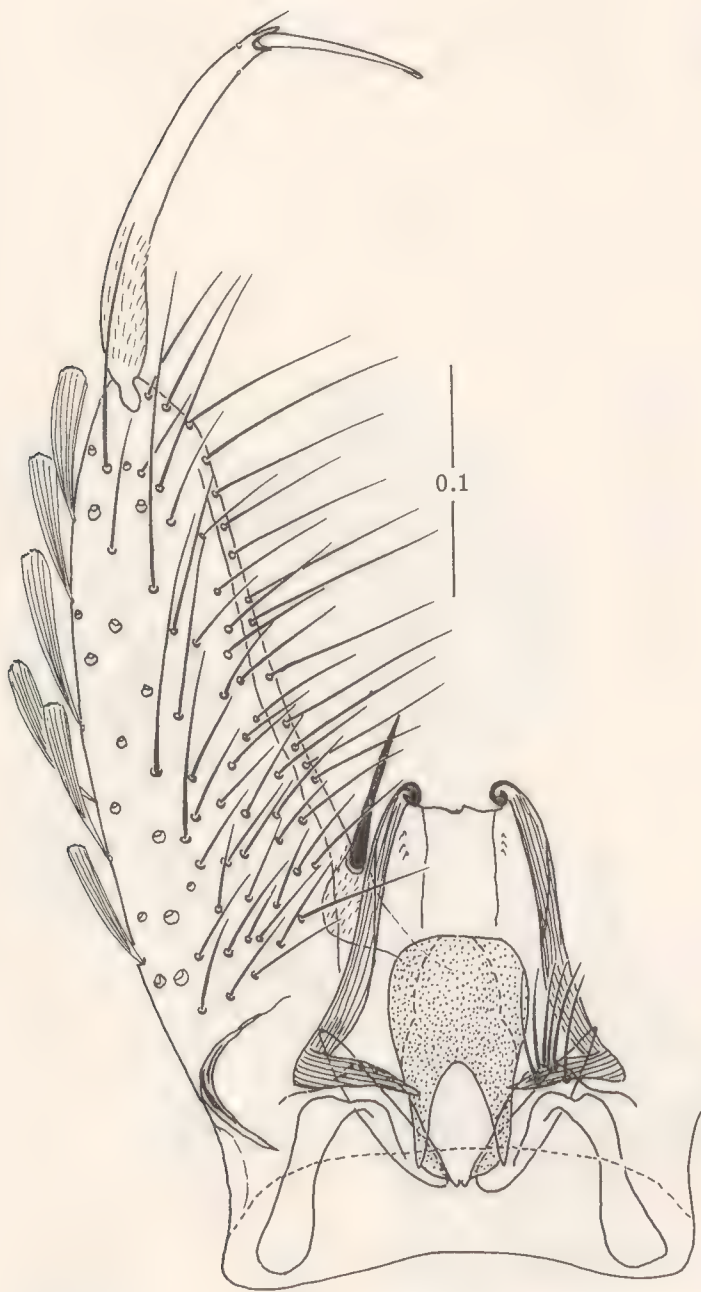
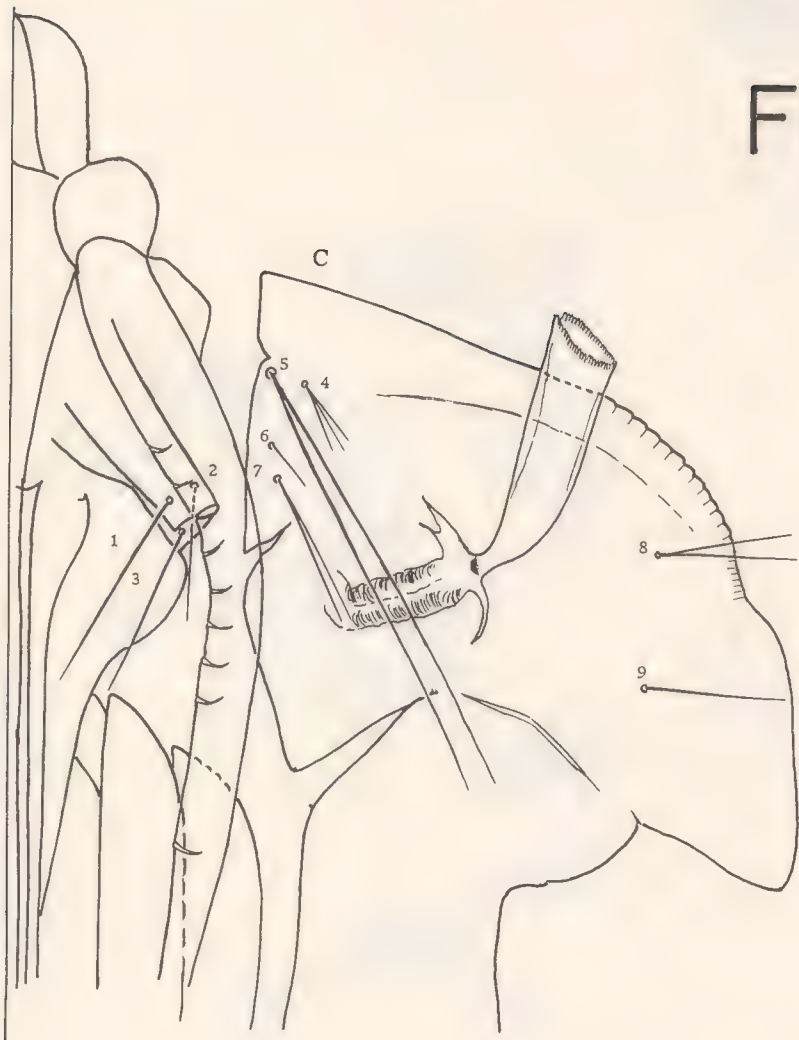


Fig.42

CR 13-111
Cervantes
Cartago
Costa Rica

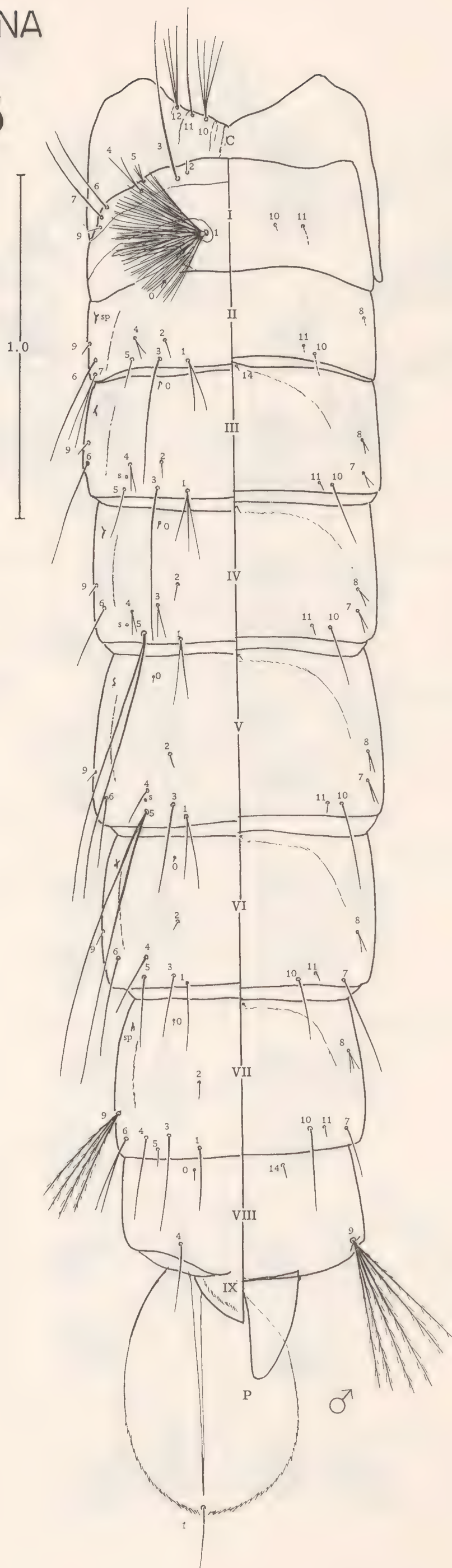
HOWARDINA

Fig.43



sexlineatus

TR 1041
La Laja Trace
Arima
St. George
Trinidad



HOWARDINA

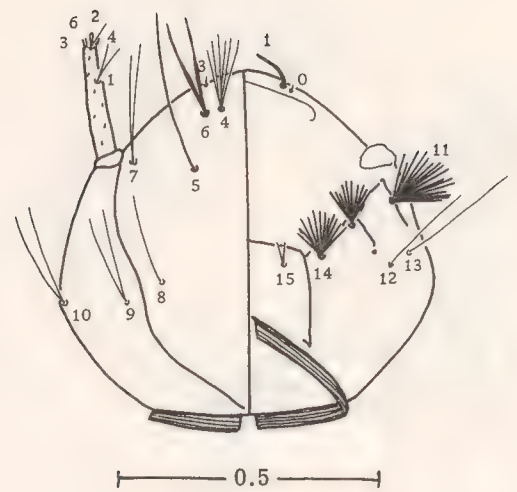
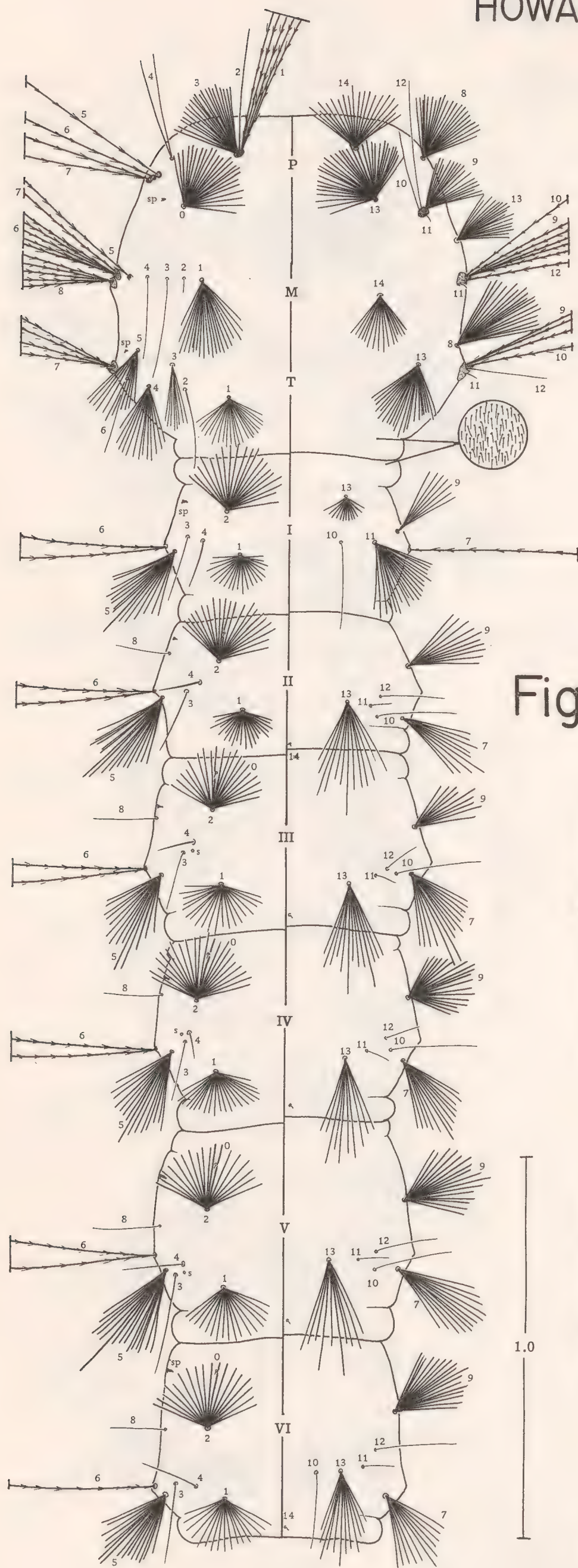
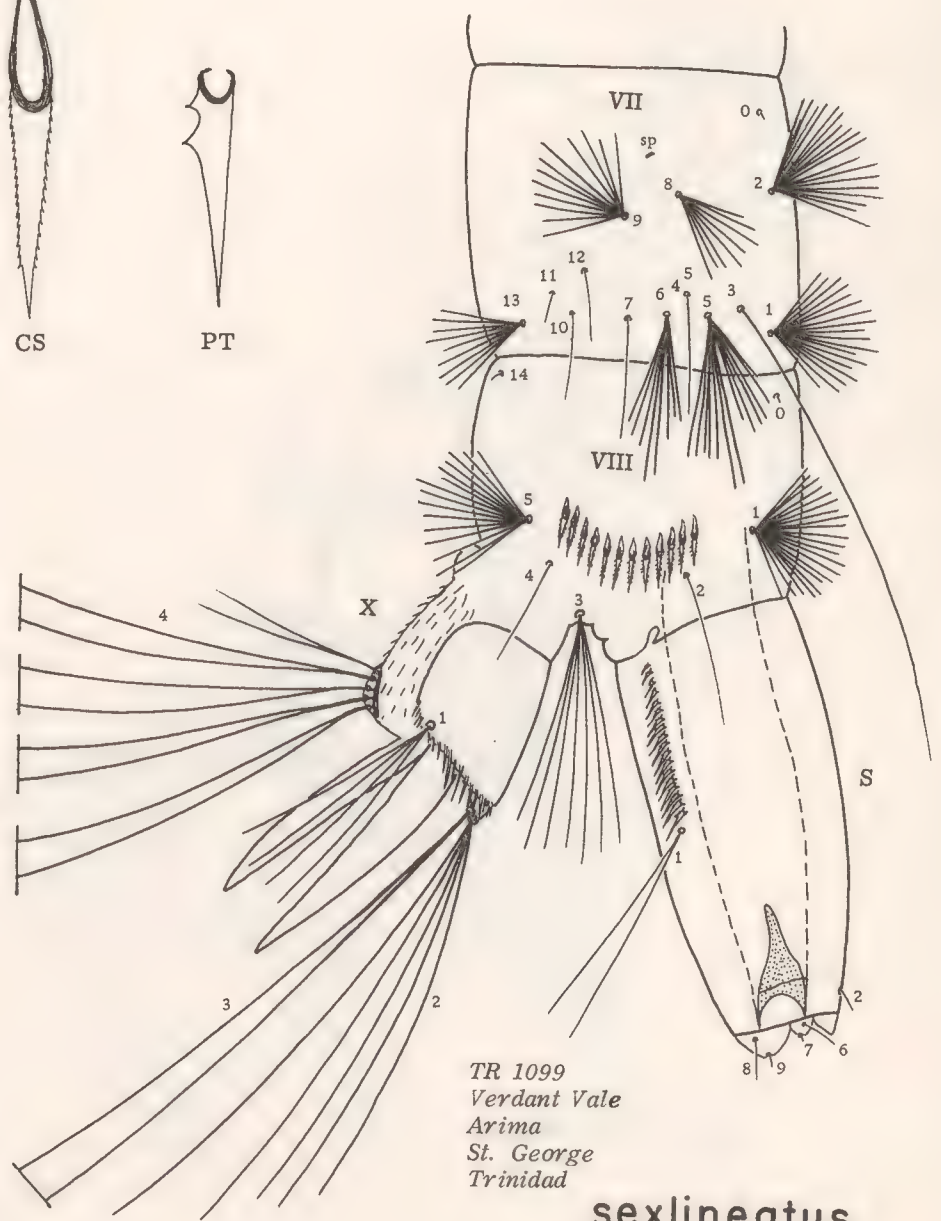
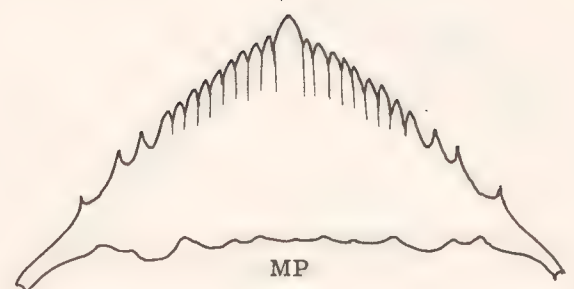


Fig. 44

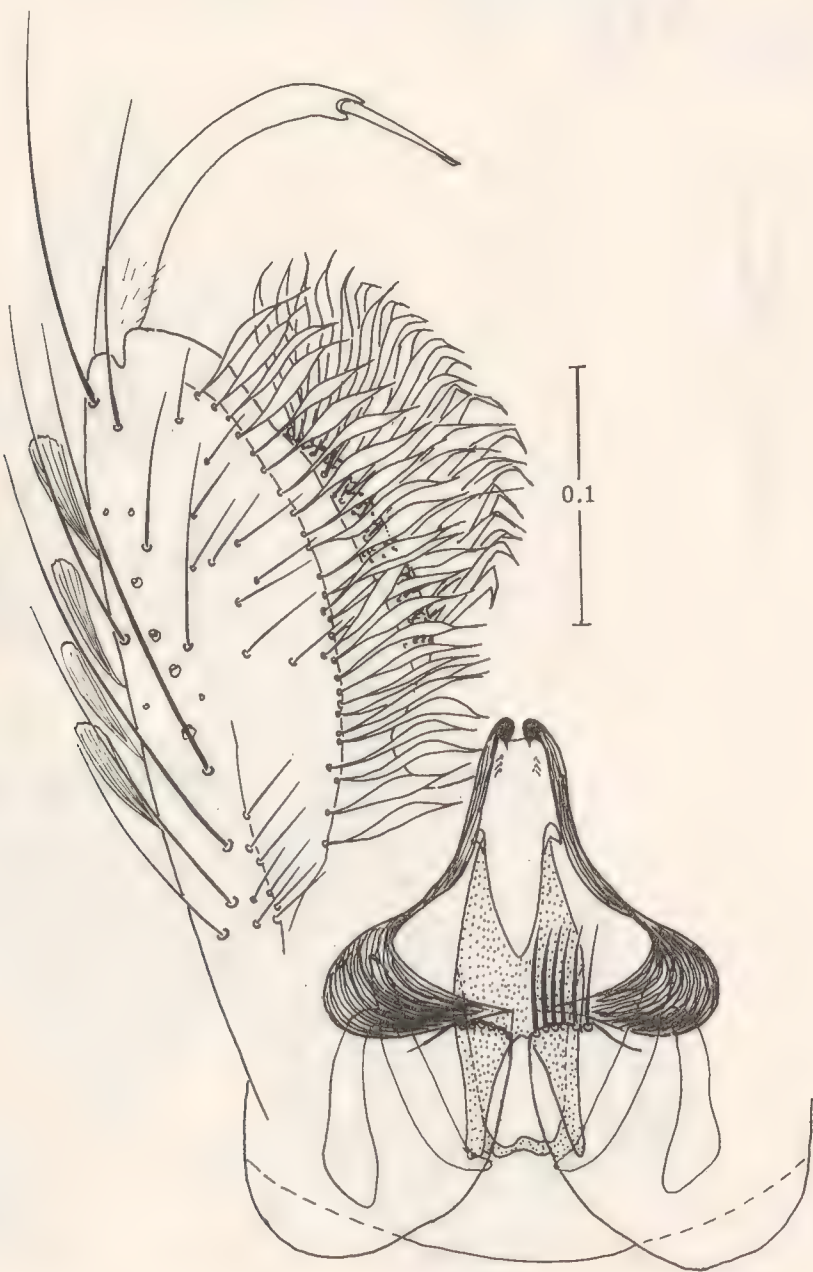
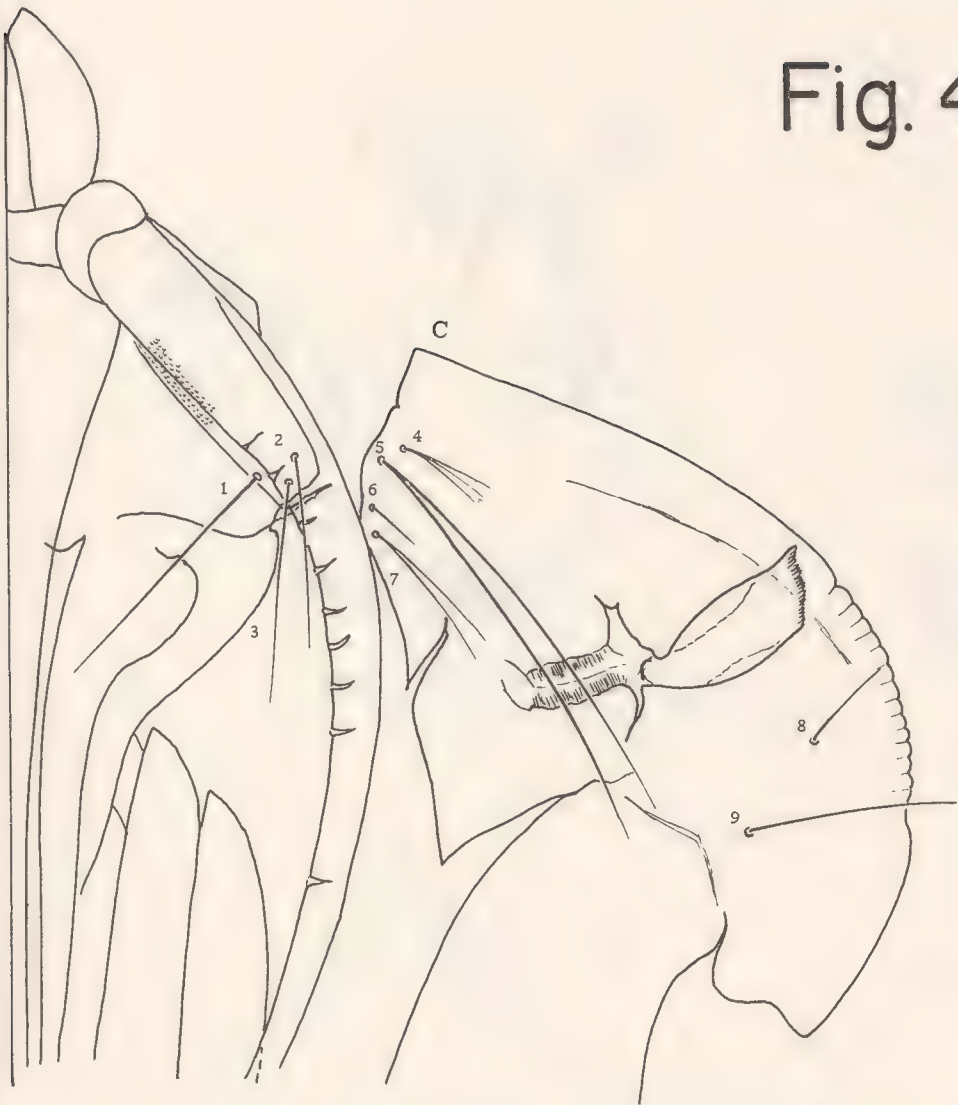


TR 1099
Verdant Vale
Arima
St. George
Trinidad

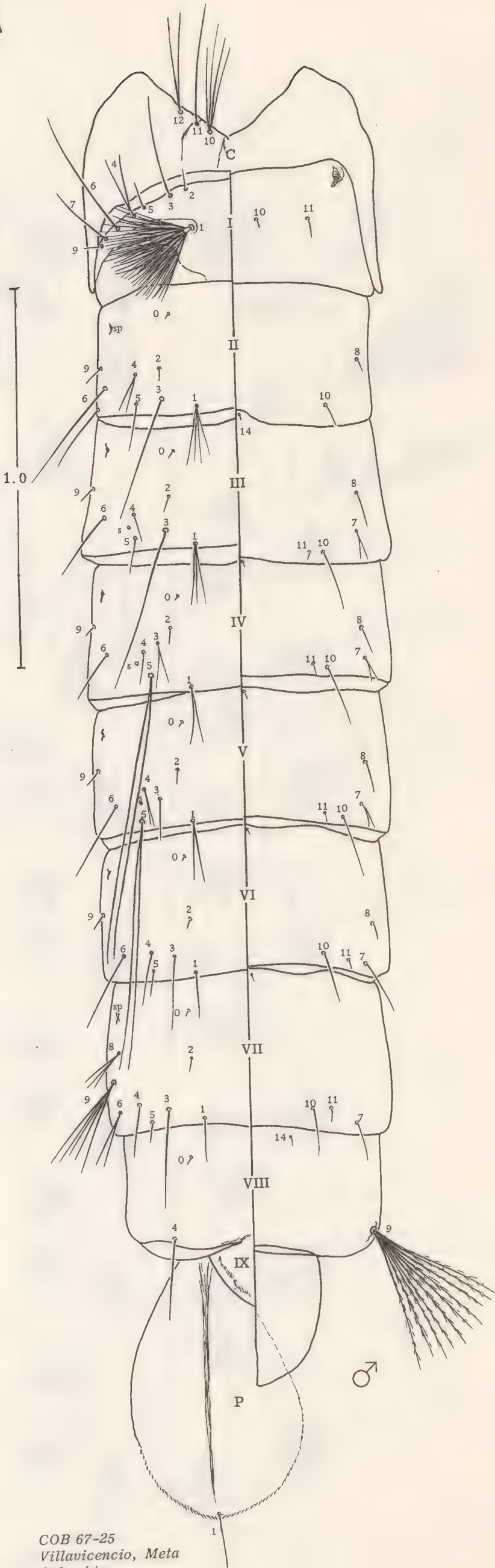
sexlineatus

HOWARDINA

Fig. 45

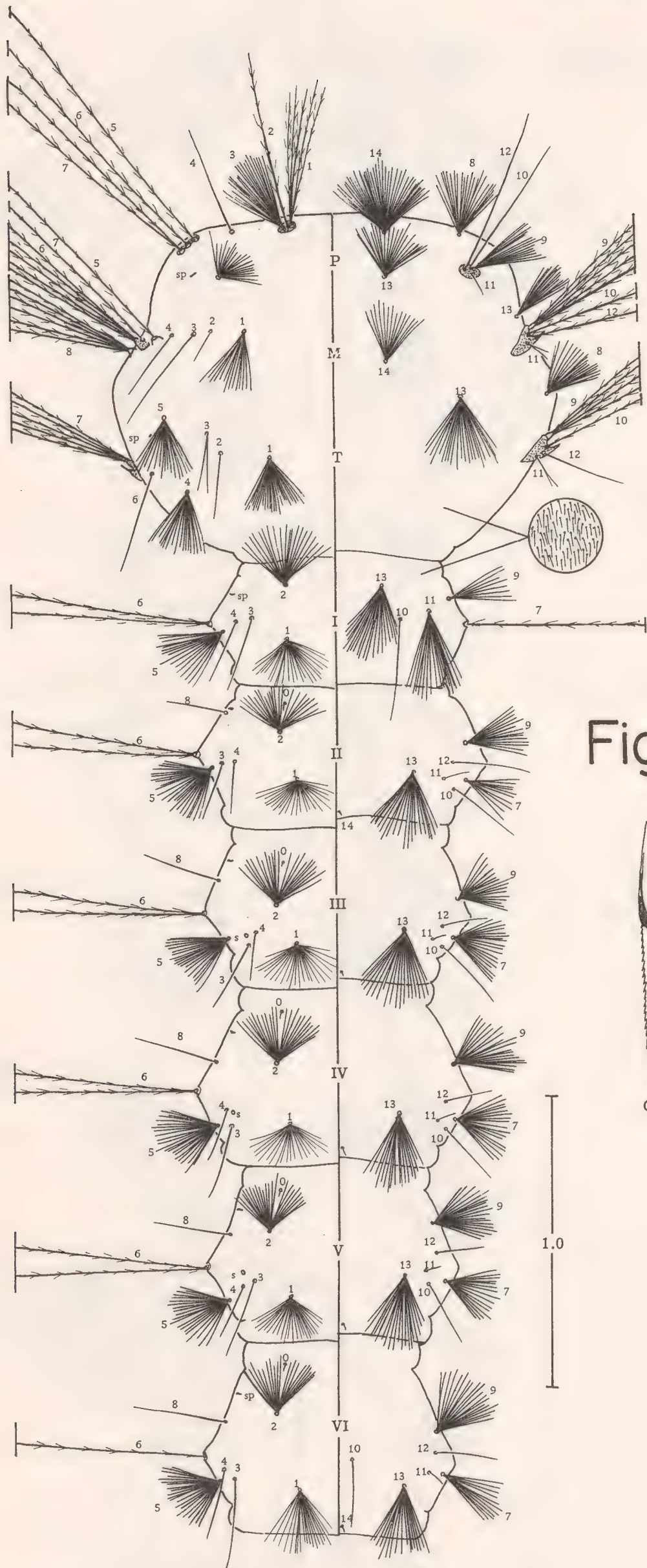


whitmorei



COB 67-25
Villavicencio, Meta
Colombia

HOWARDINA



COB 68
Buena Vista
Villavicencio, Meta
Colombia

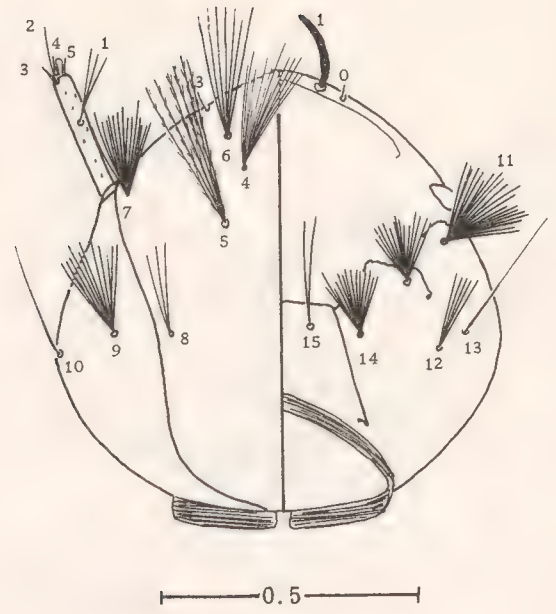
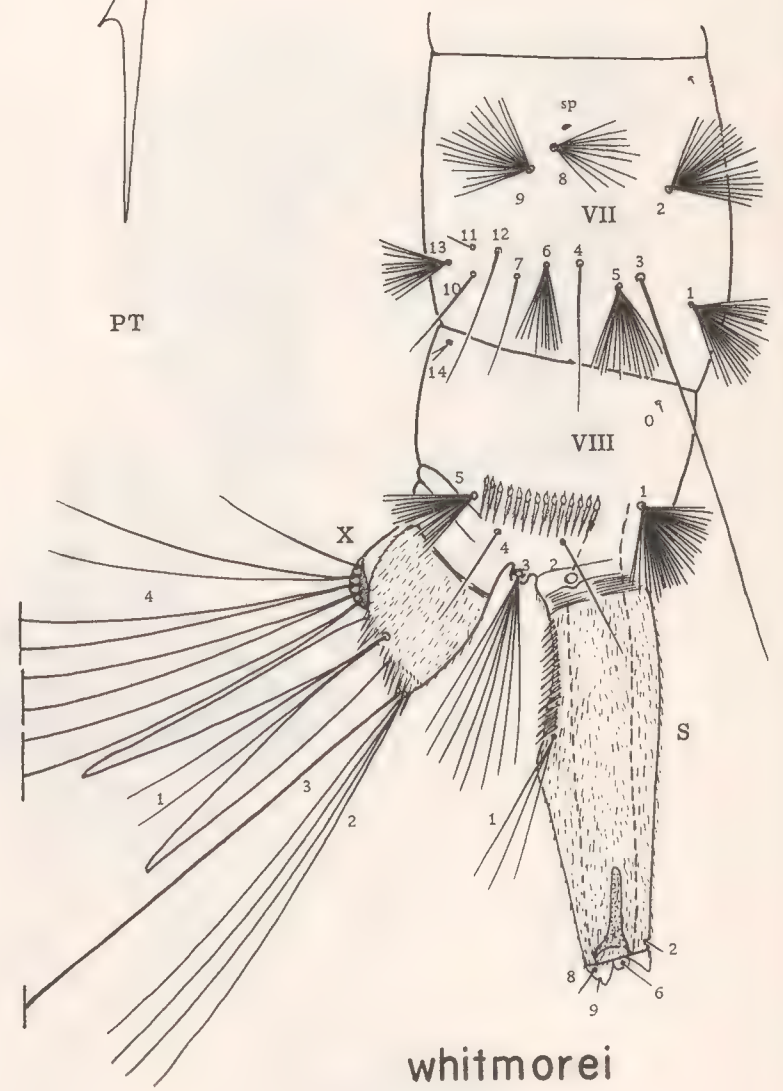
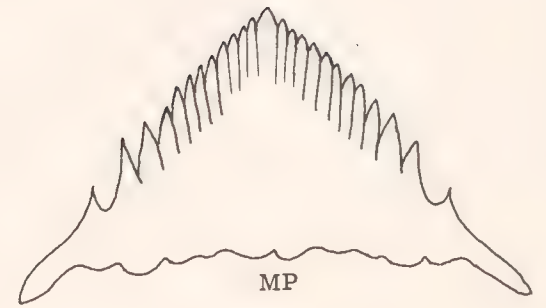


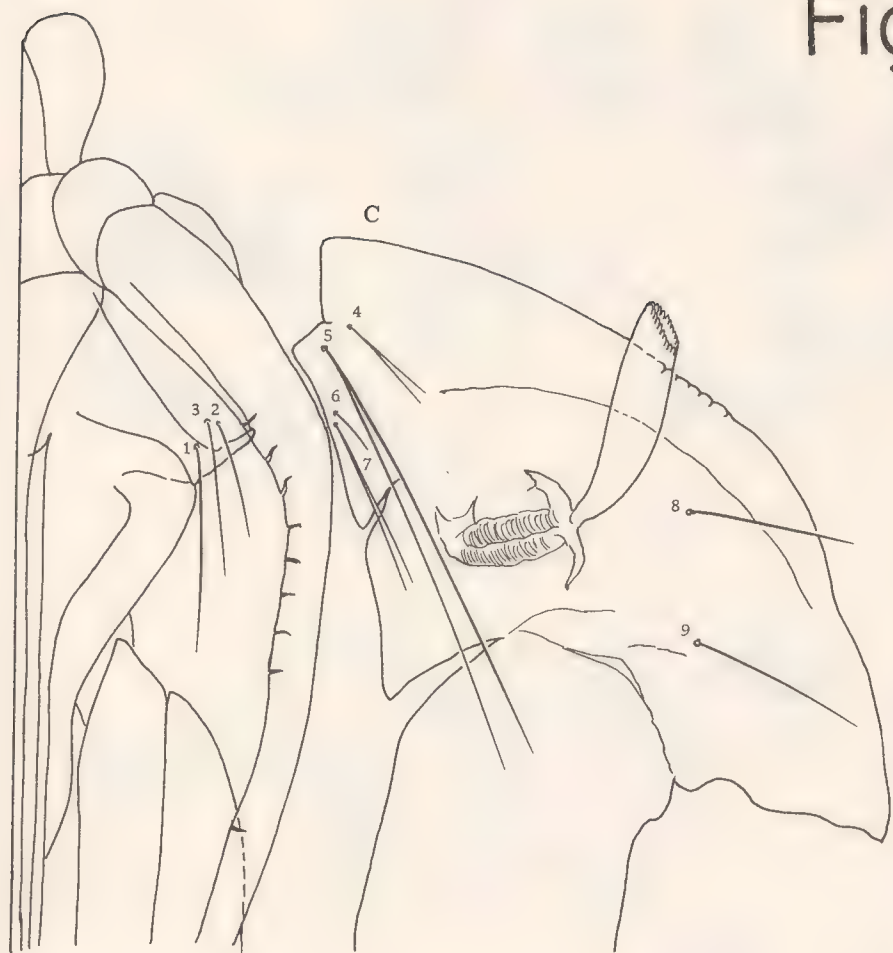
Fig. 46



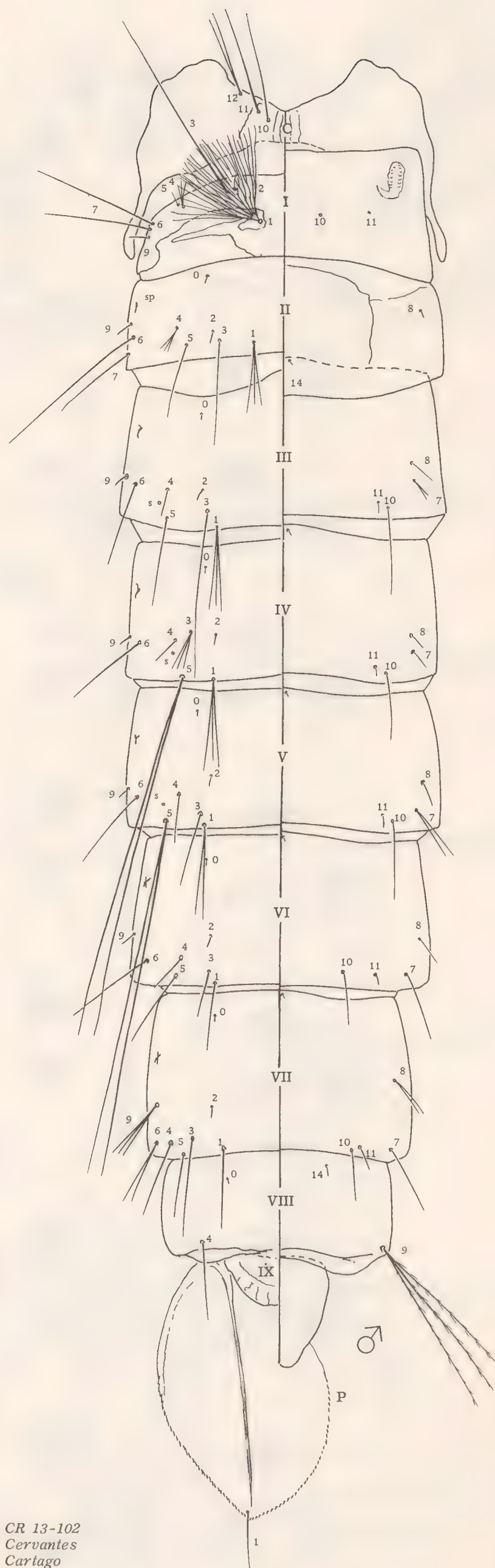
whitmorei

HOWARDINA

Fig. 47



allotecnnon



CR 13-102
Cervantes
Cartago
Costa Rica

HOWARDINA

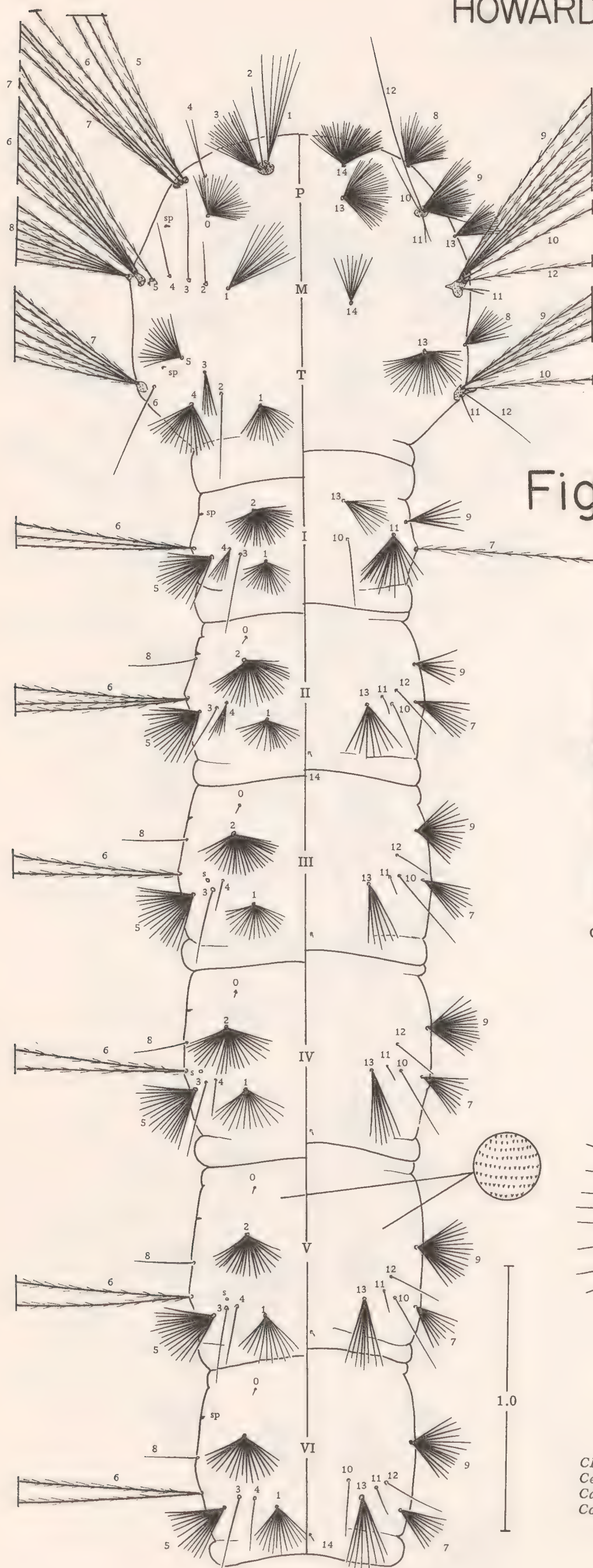
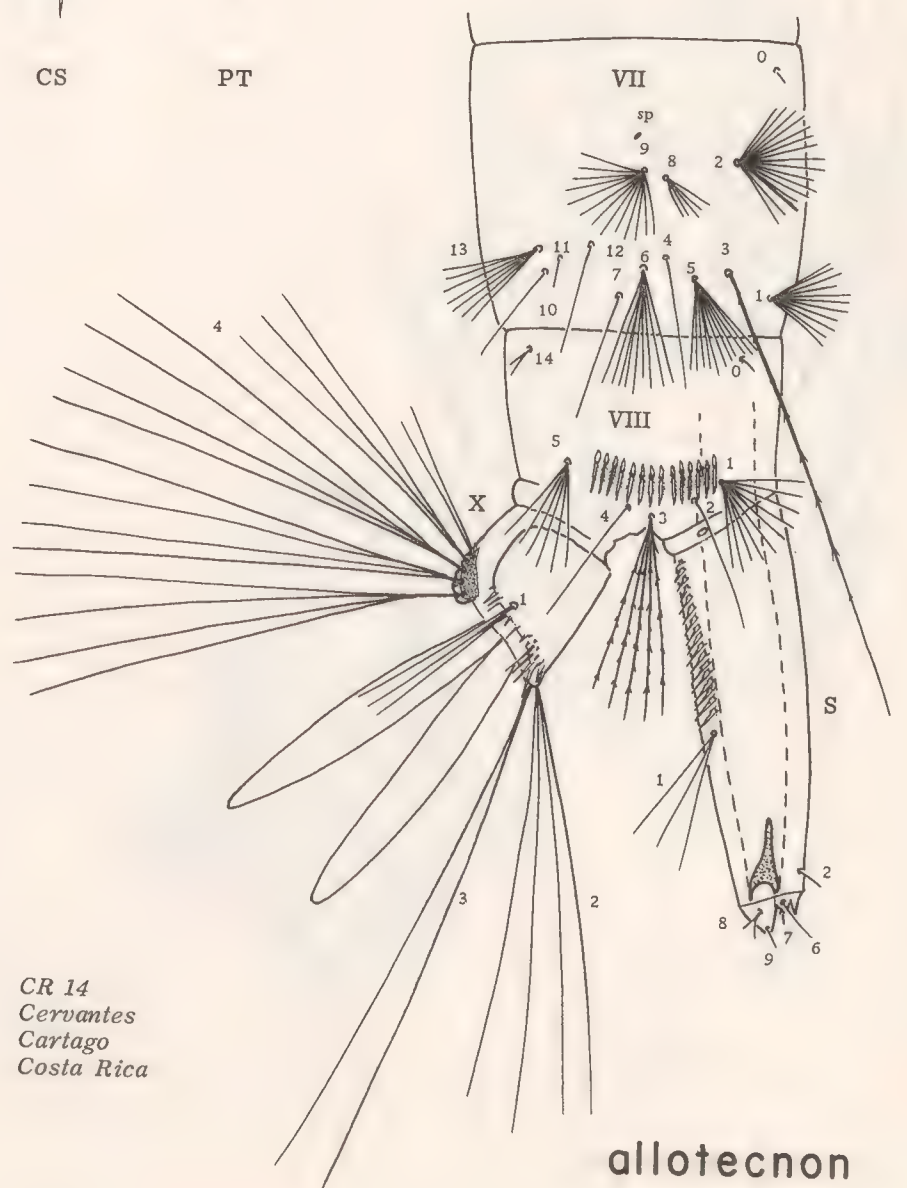
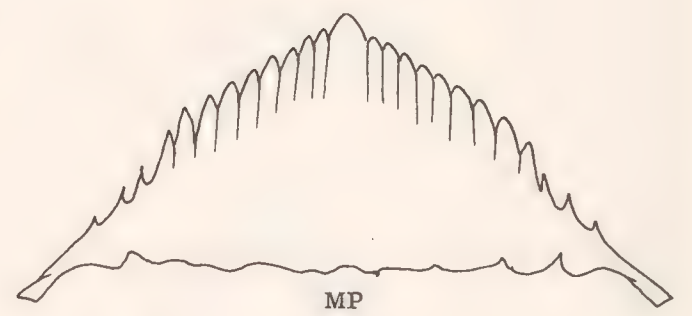
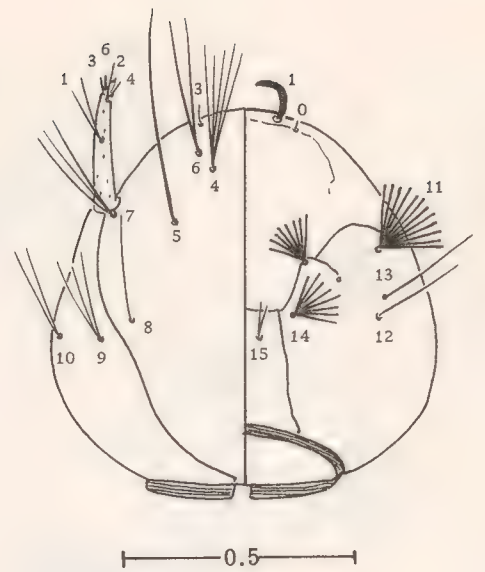


Fig. 48



CR 14
Cervantes
Cartago
Costa Rica

HOWARDINA

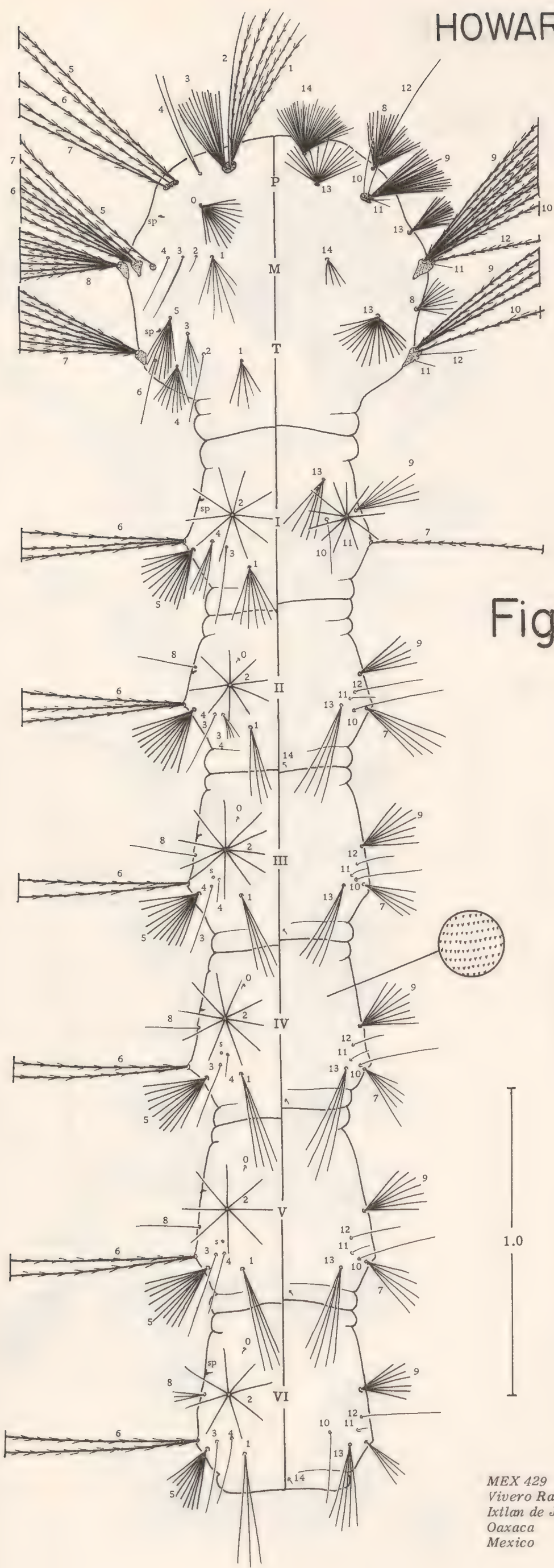
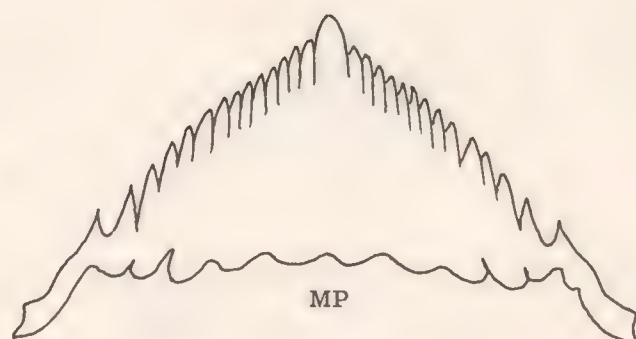
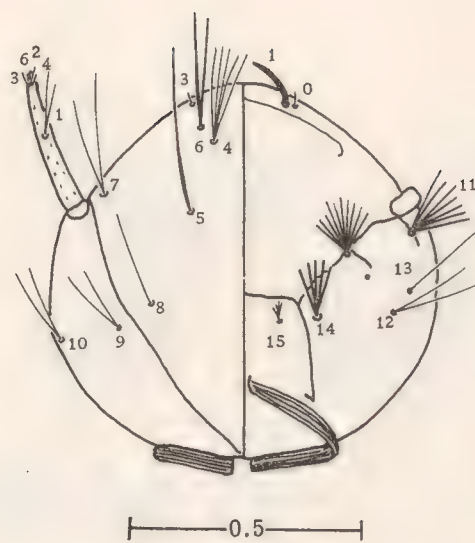
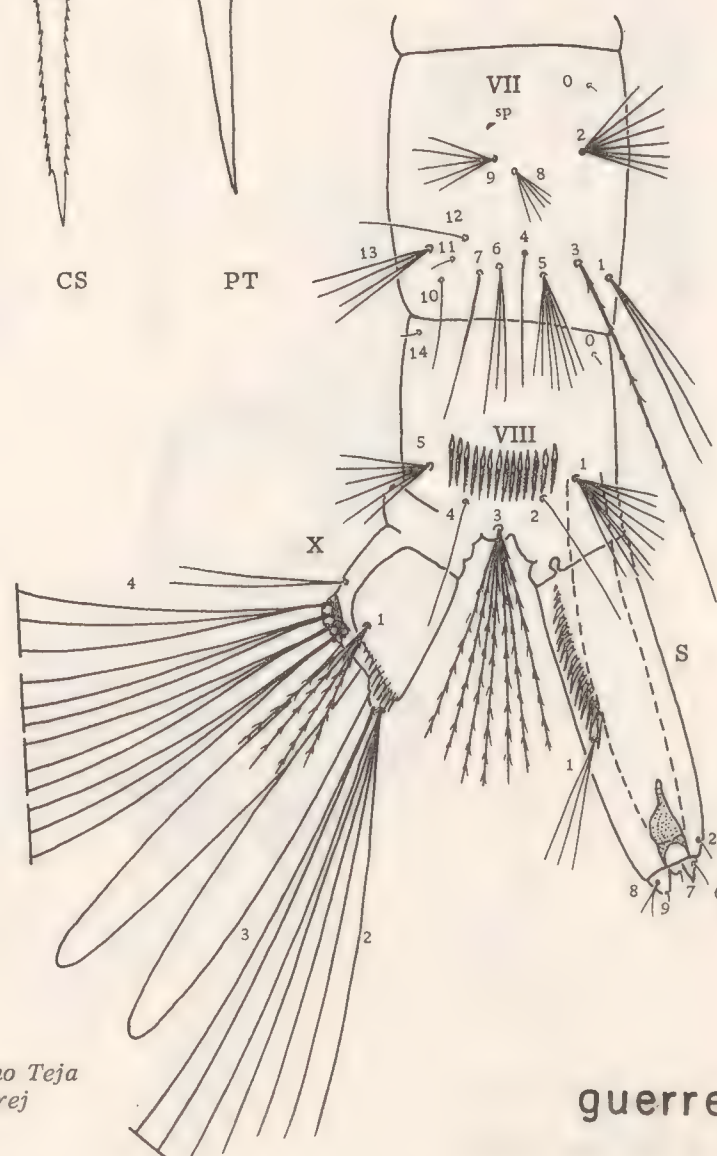


Fig. 49



CS

PT

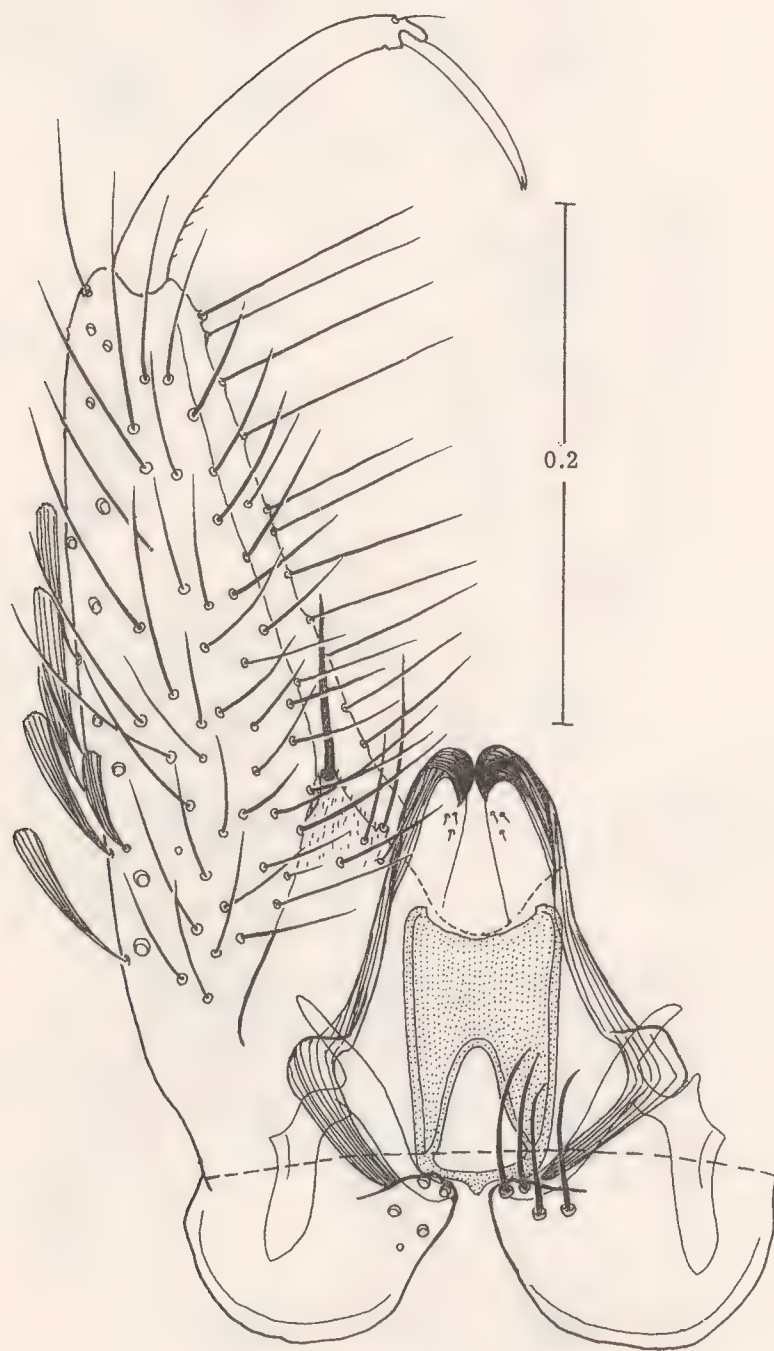
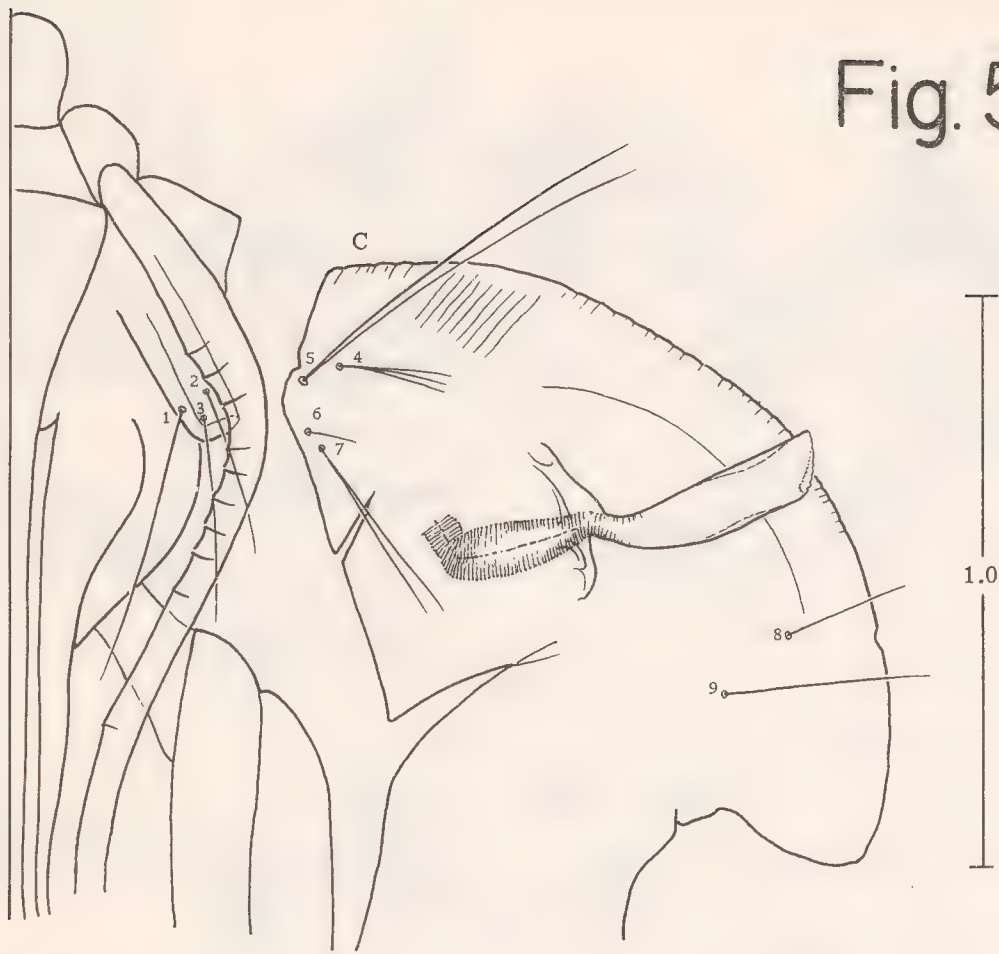


guerrero

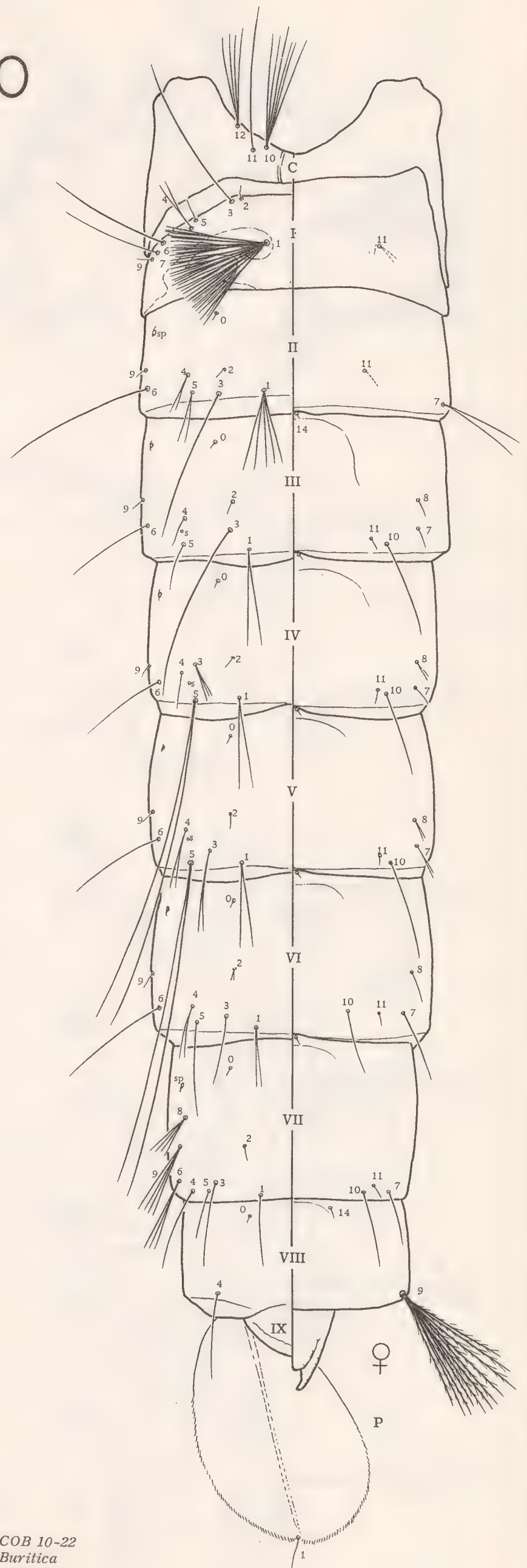
MEX 429
Vivero Rancho Teja
Ixtilan de Juarez
Oaxaca
Mexico

HOWARDINA

Fig. 50



eleanorae



COB 10-22
Buritica
Antioquia
Colombia

HOWARDINA

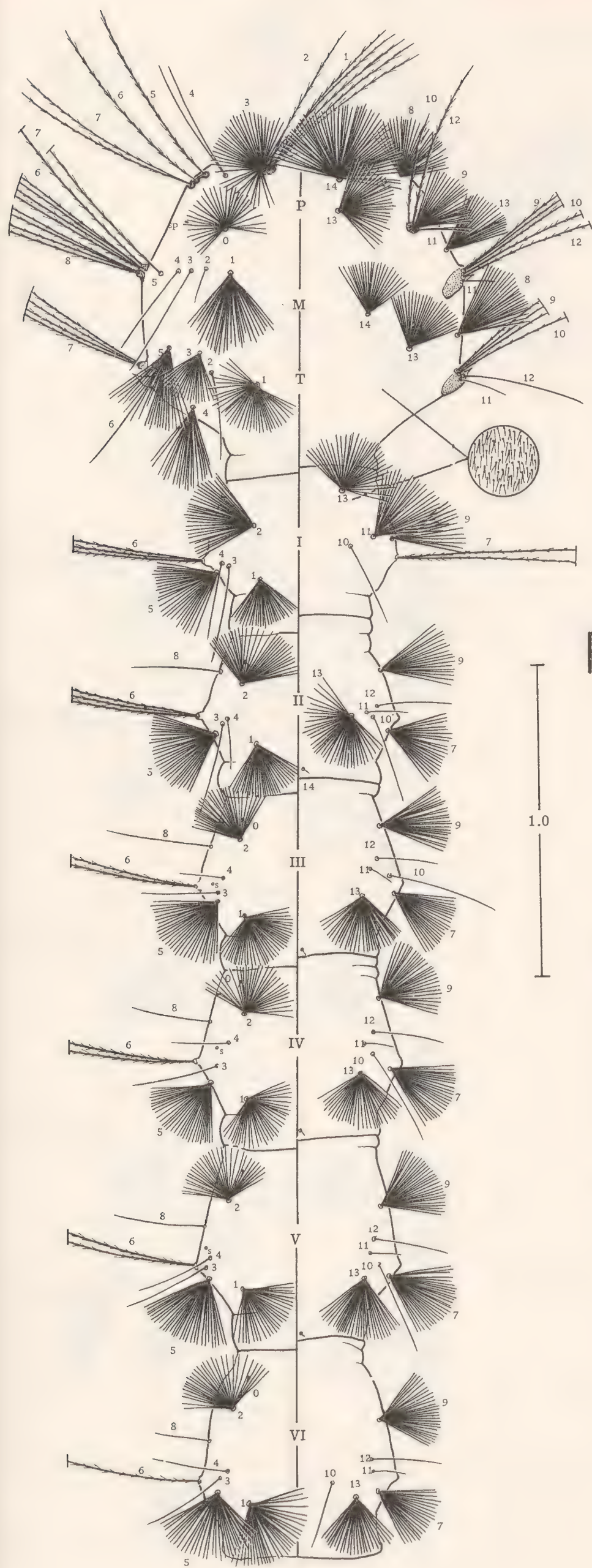
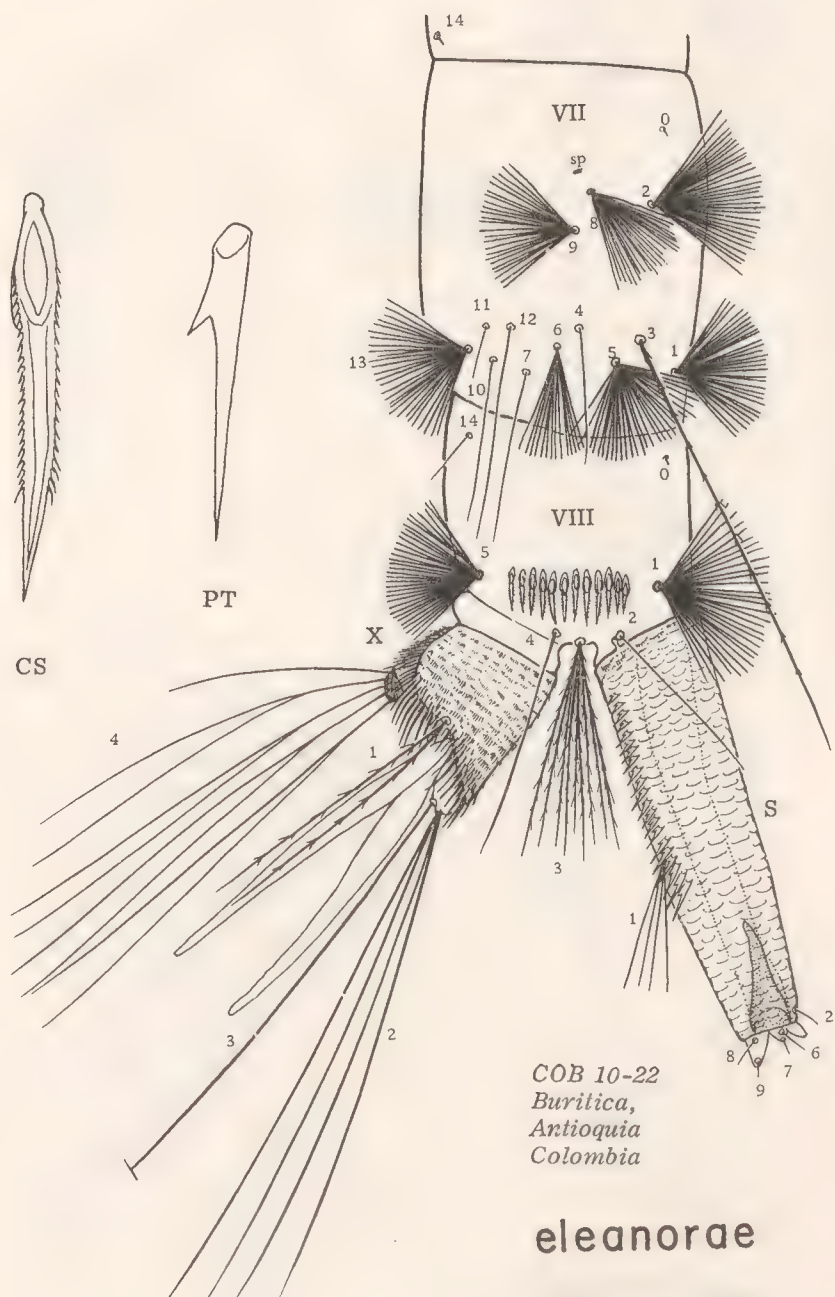
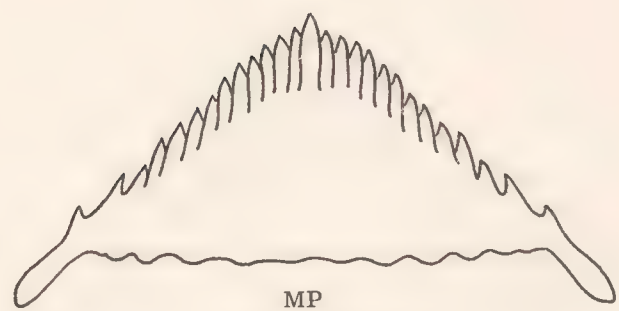
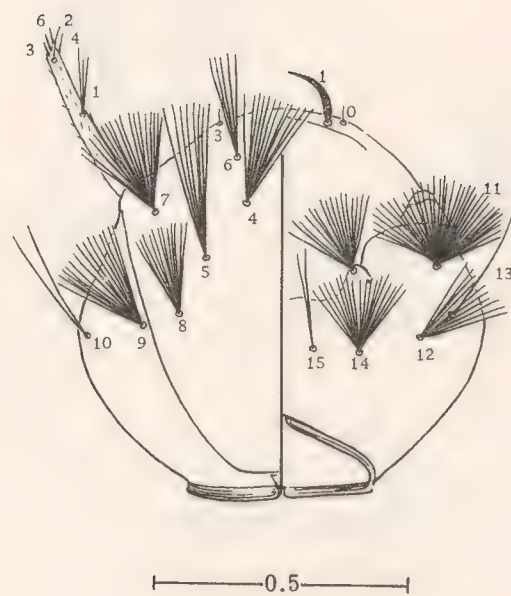
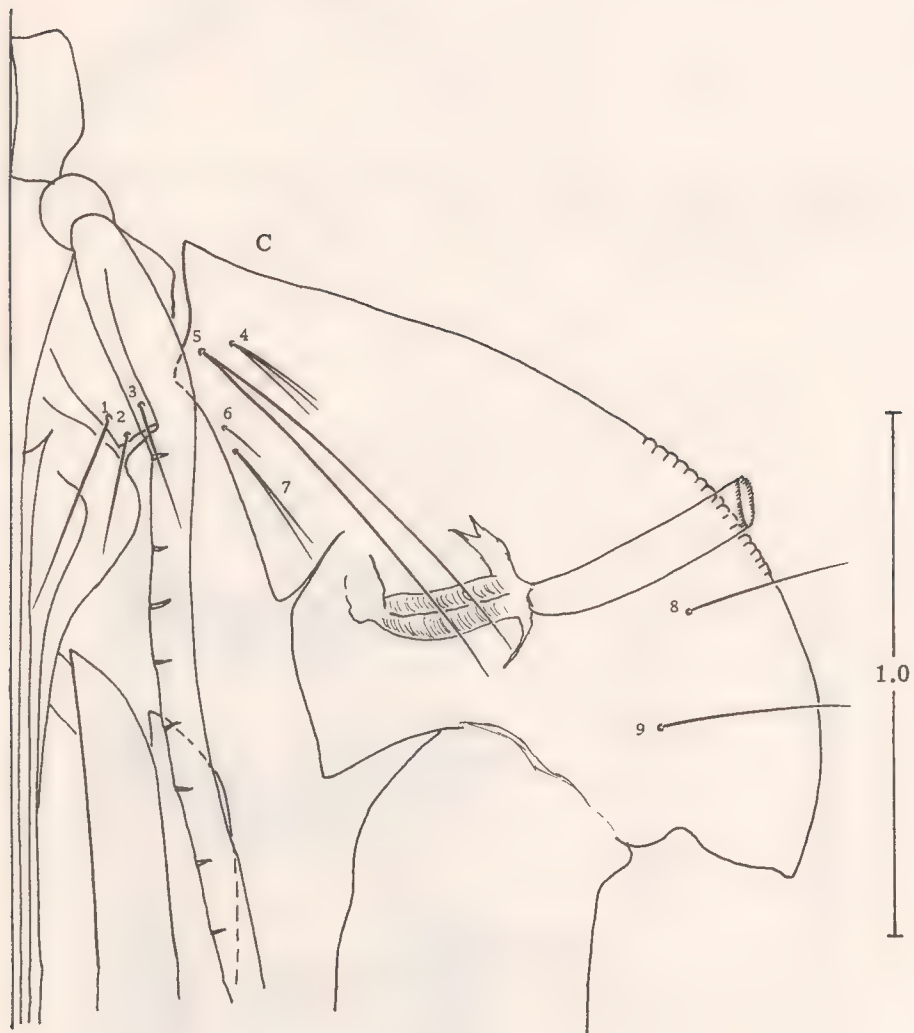


Fig. 51



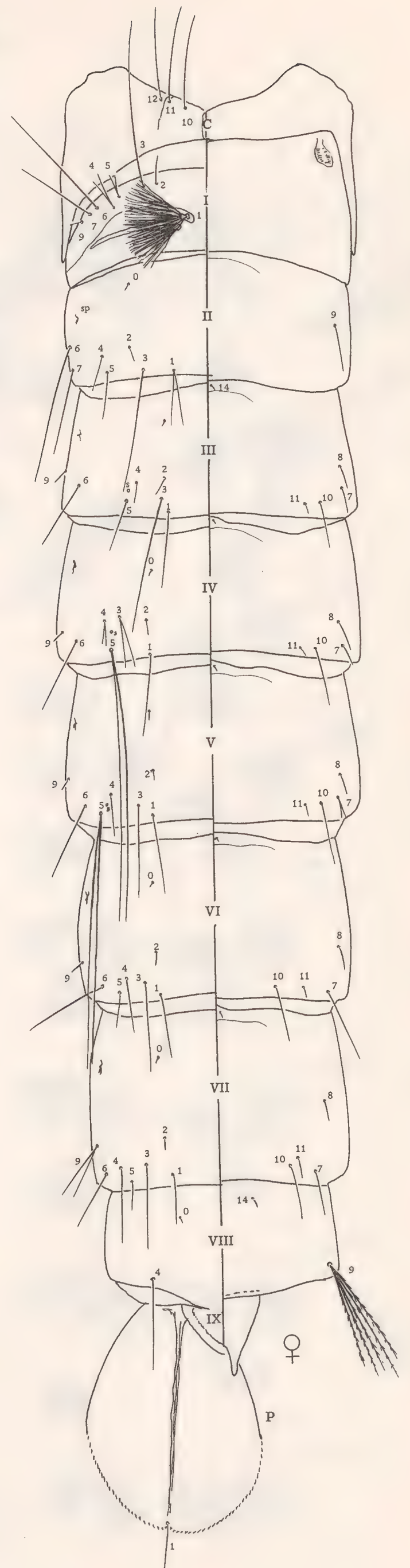
HOWARDINA

Fig. 52



marinkellei

COM 63-15
Suba
Bogota, Cundinamarca
Colombia



HOWARDINA

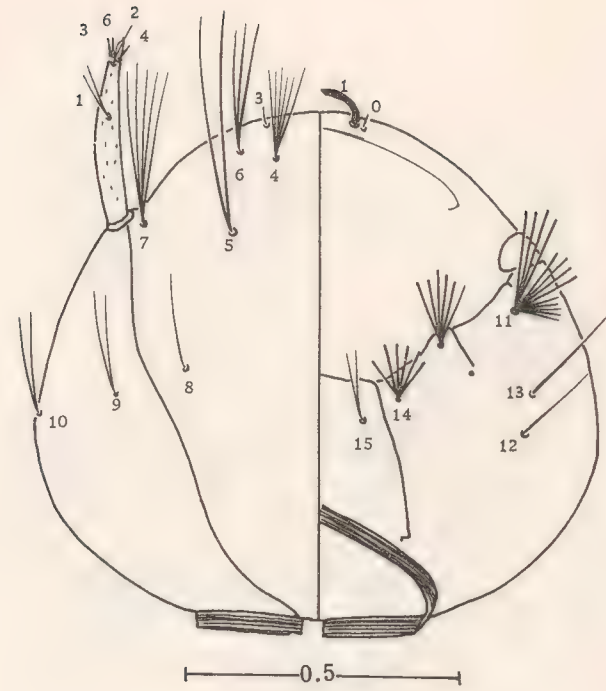
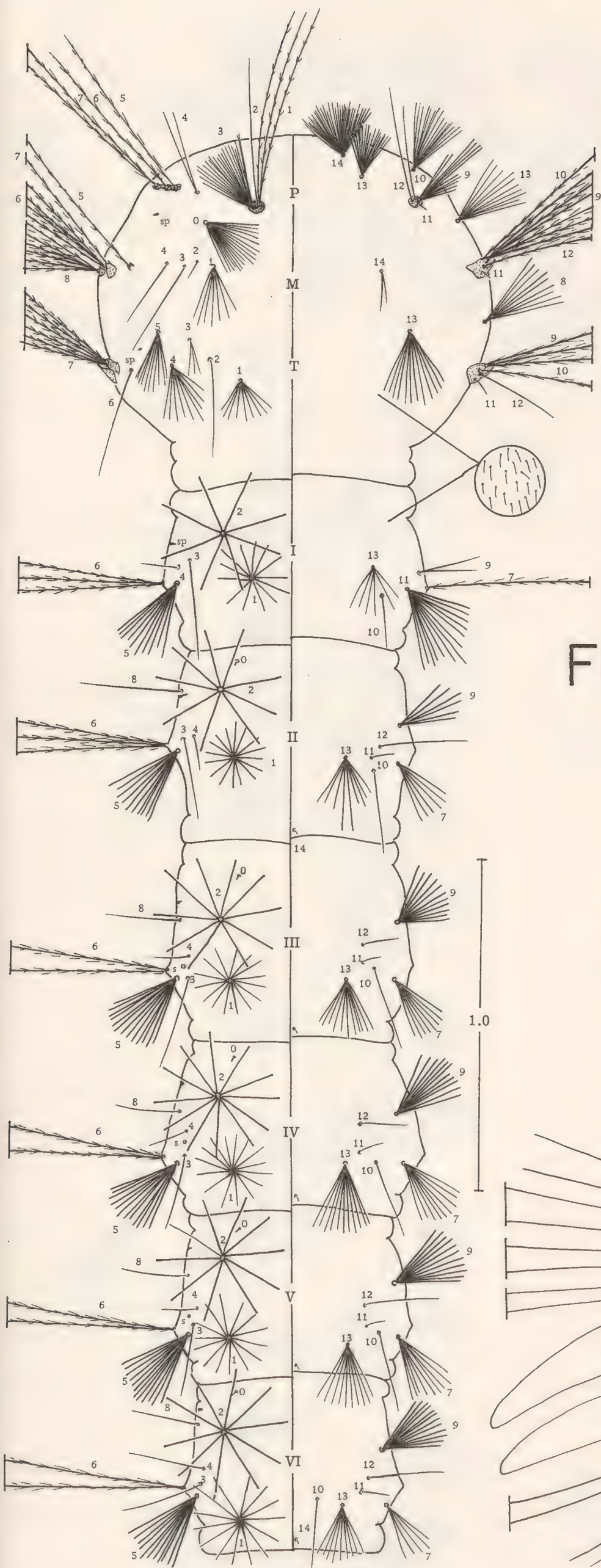
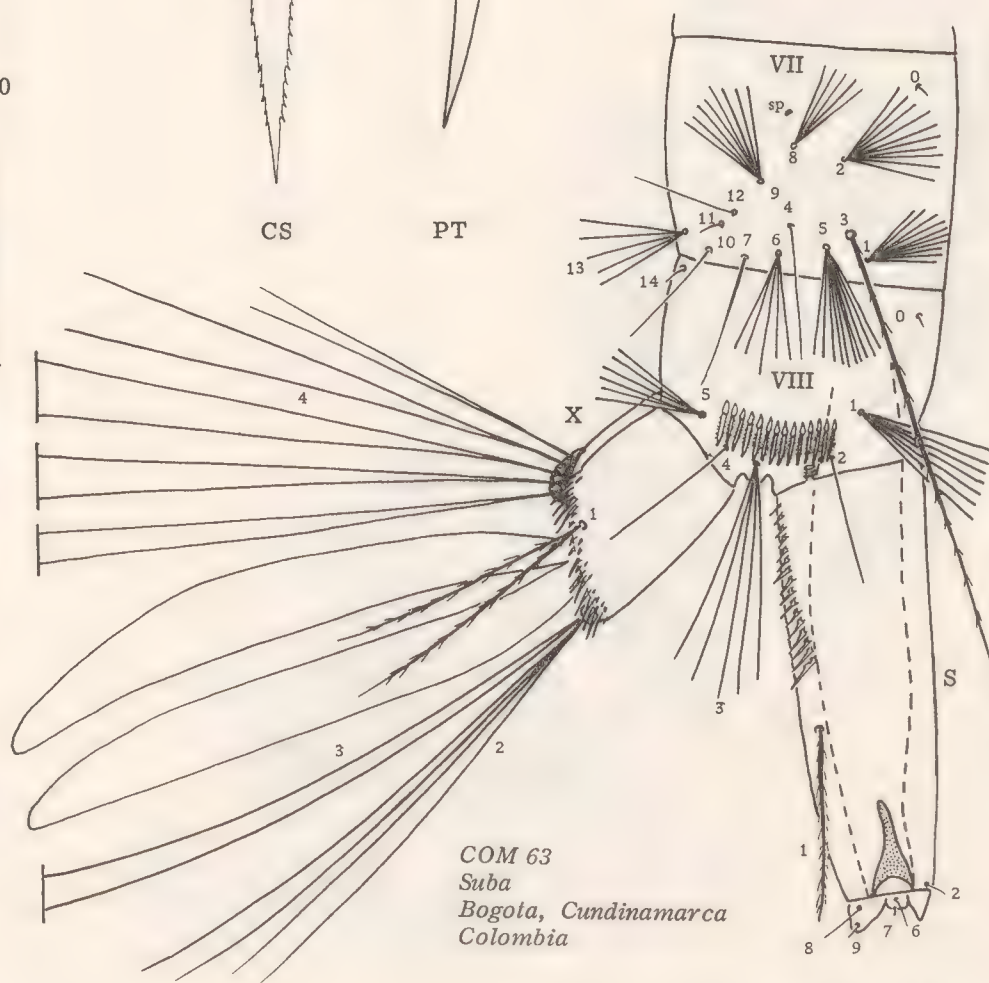
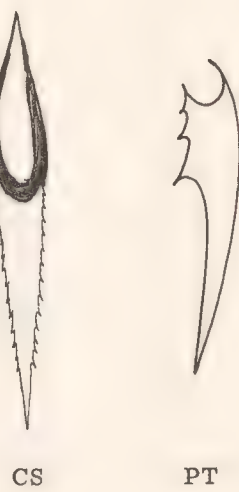
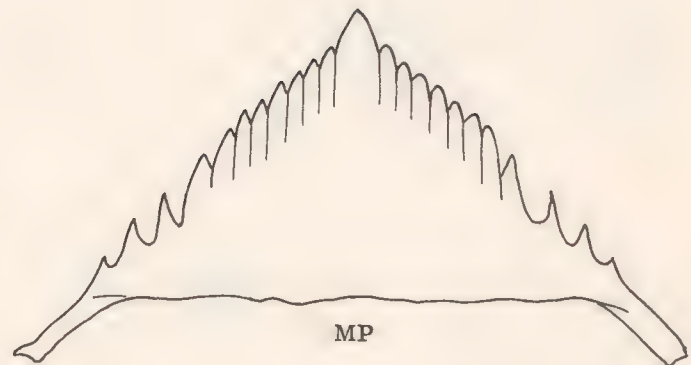


Fig. 53

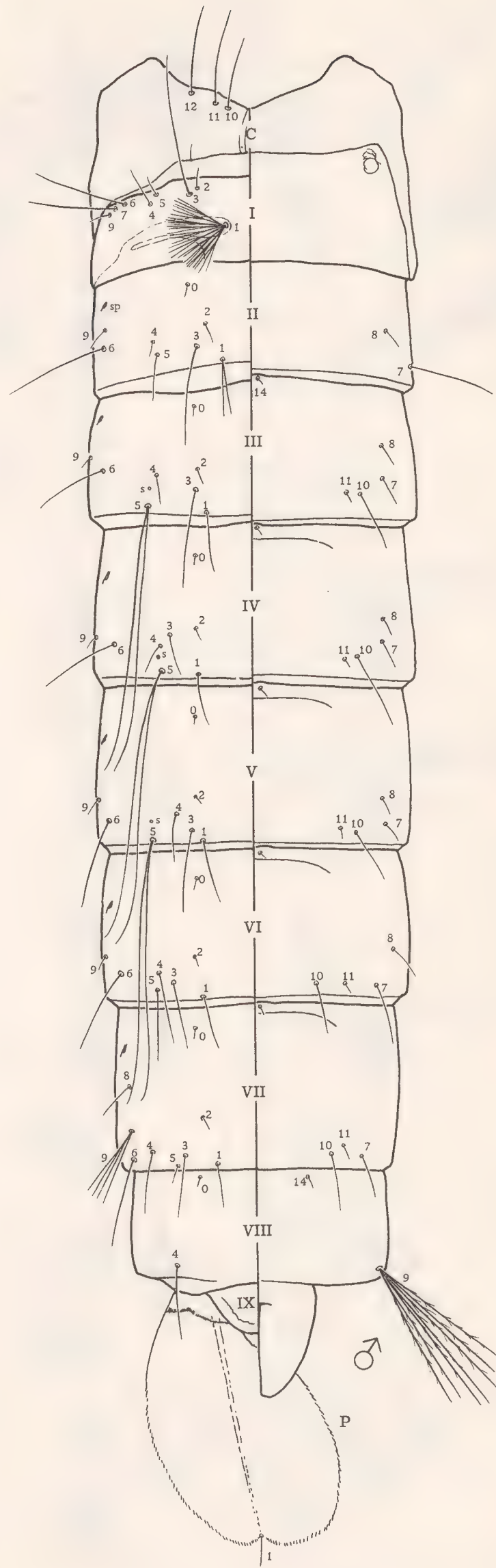
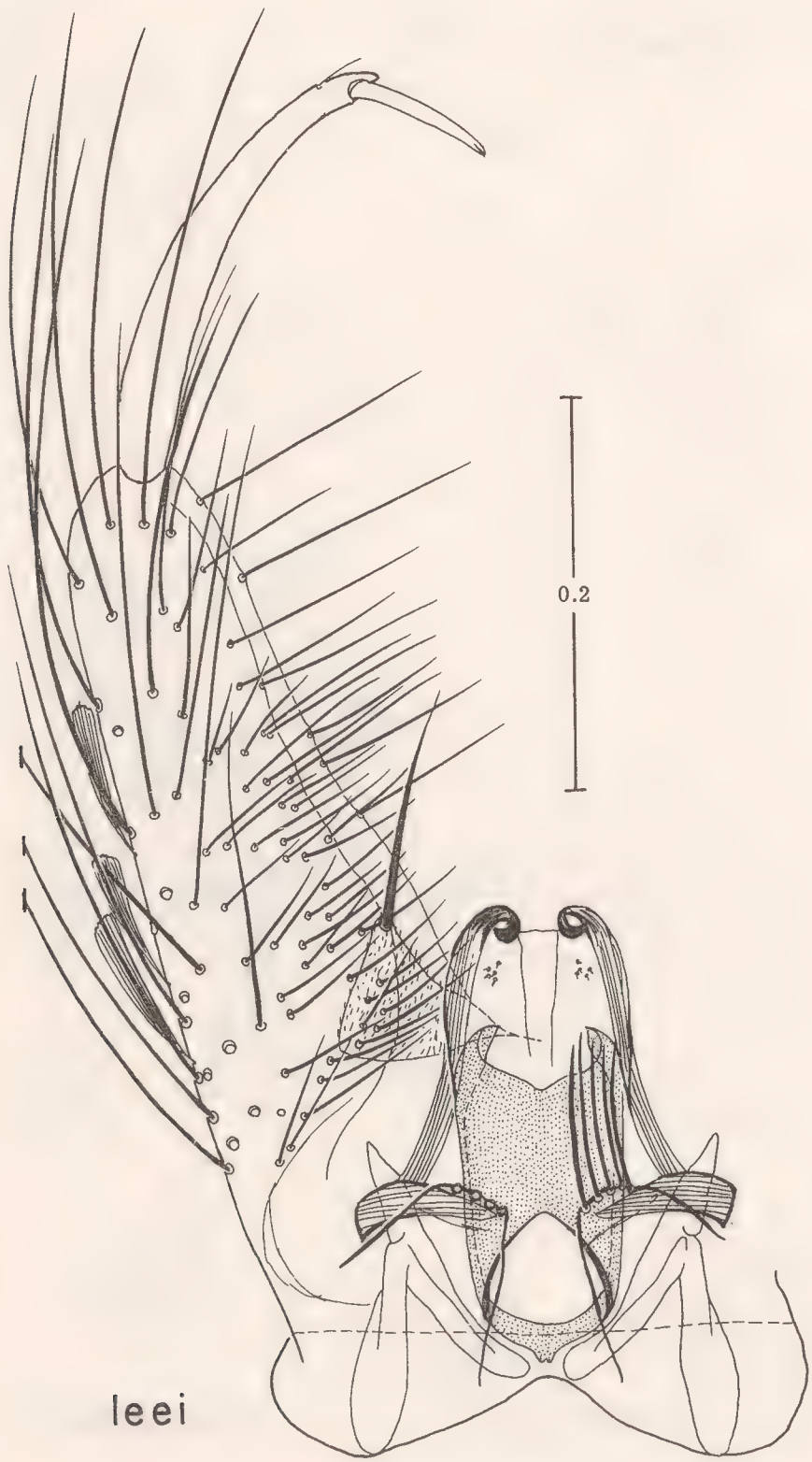
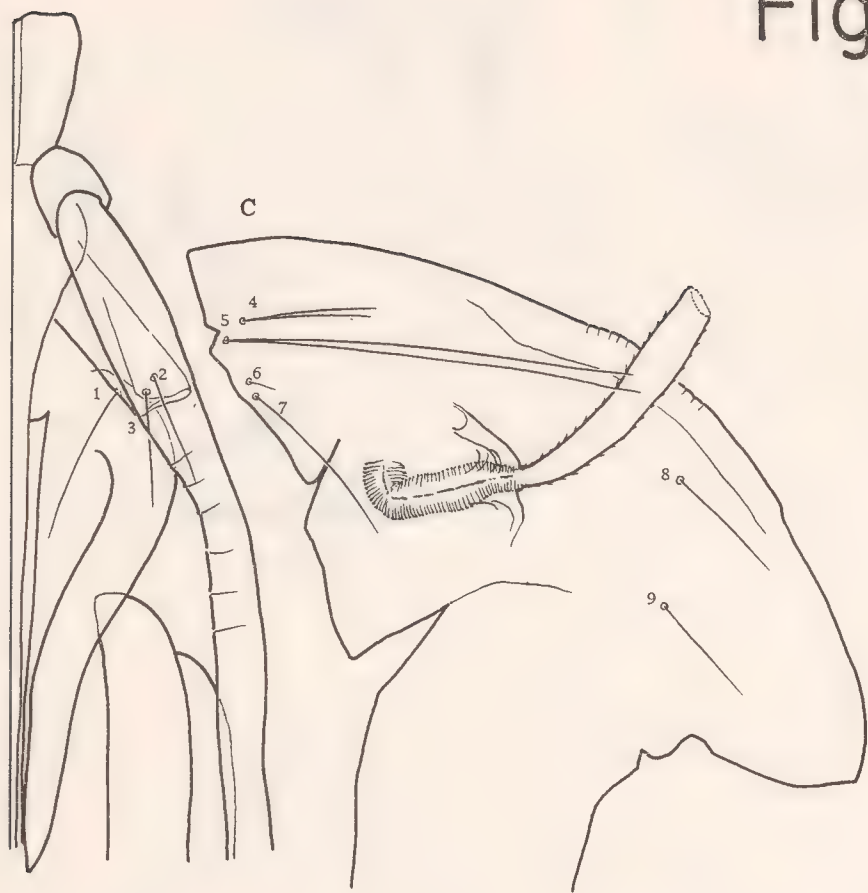


COM 63
Suba
Bogota, Cundinamarca
Colombia

marinkellei

HOWARDINA

Fig. 54



COL 16-100
Purace
Cauca
Colombia

HOWARDINA

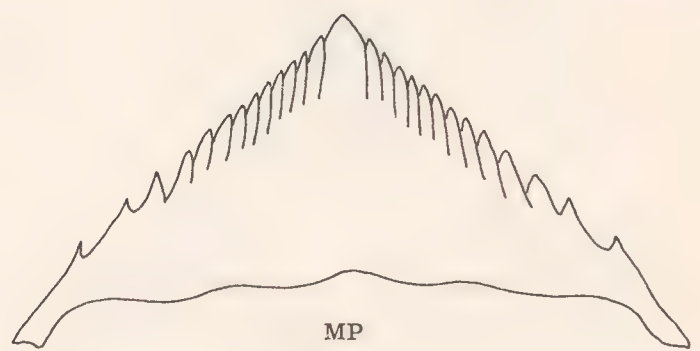
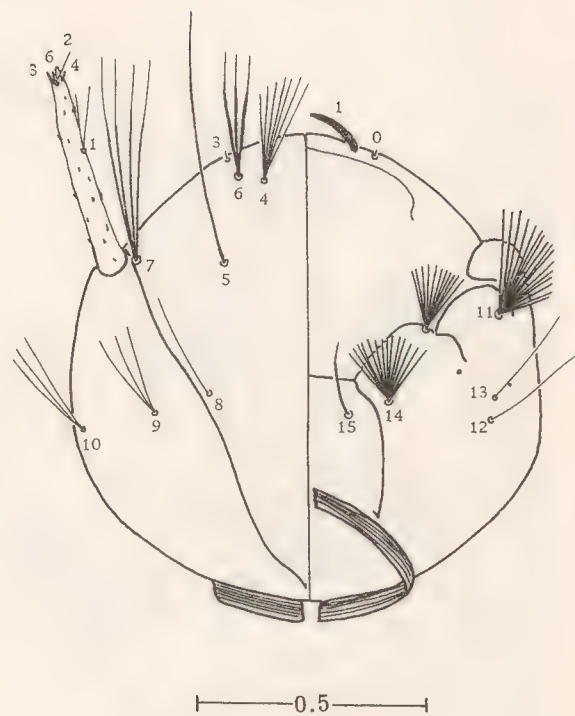
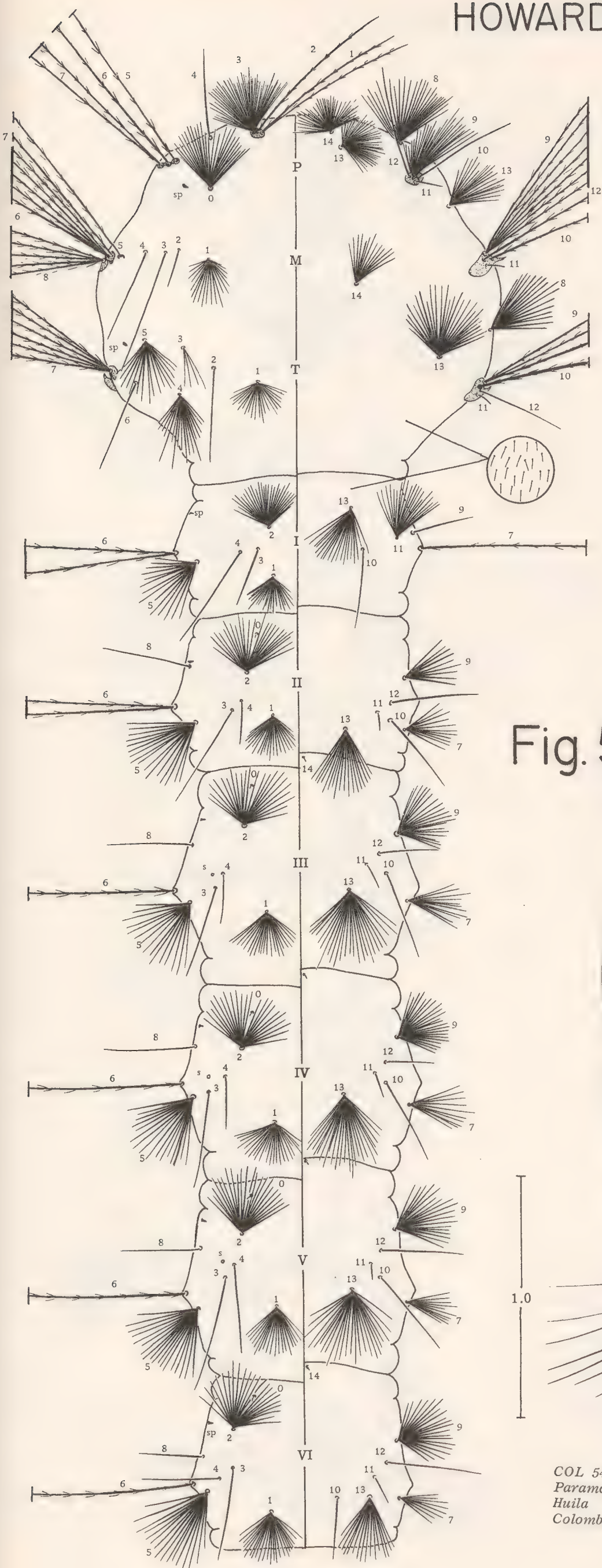
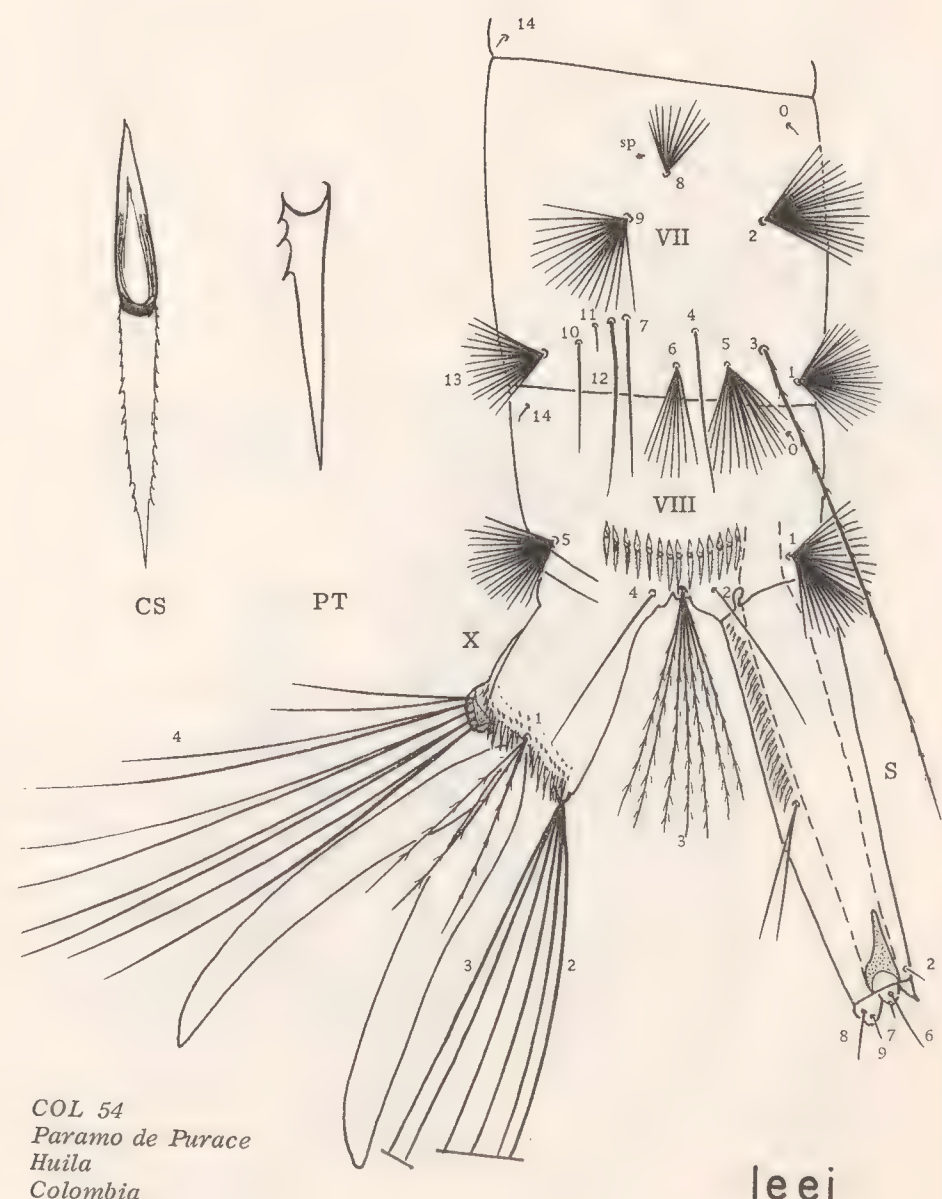


Fig. 55

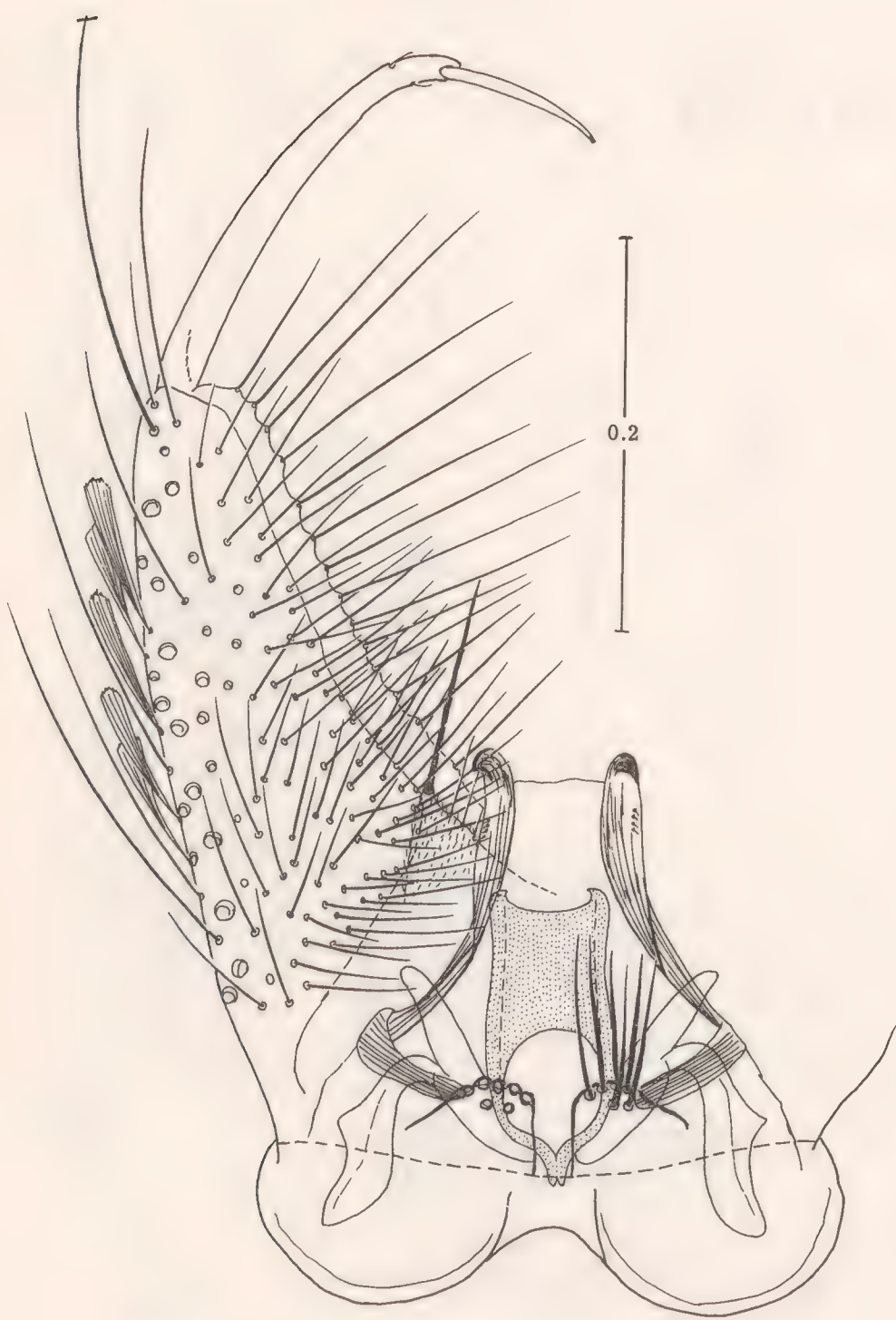
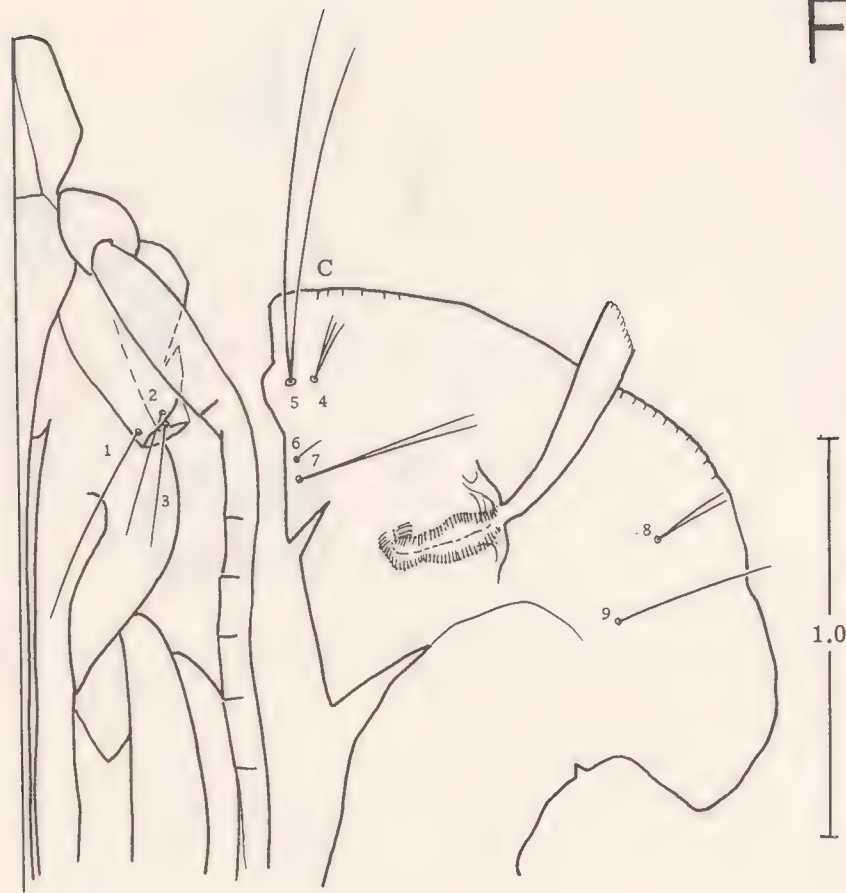


COL 54
Paramo de Purace
Huila
Colombia

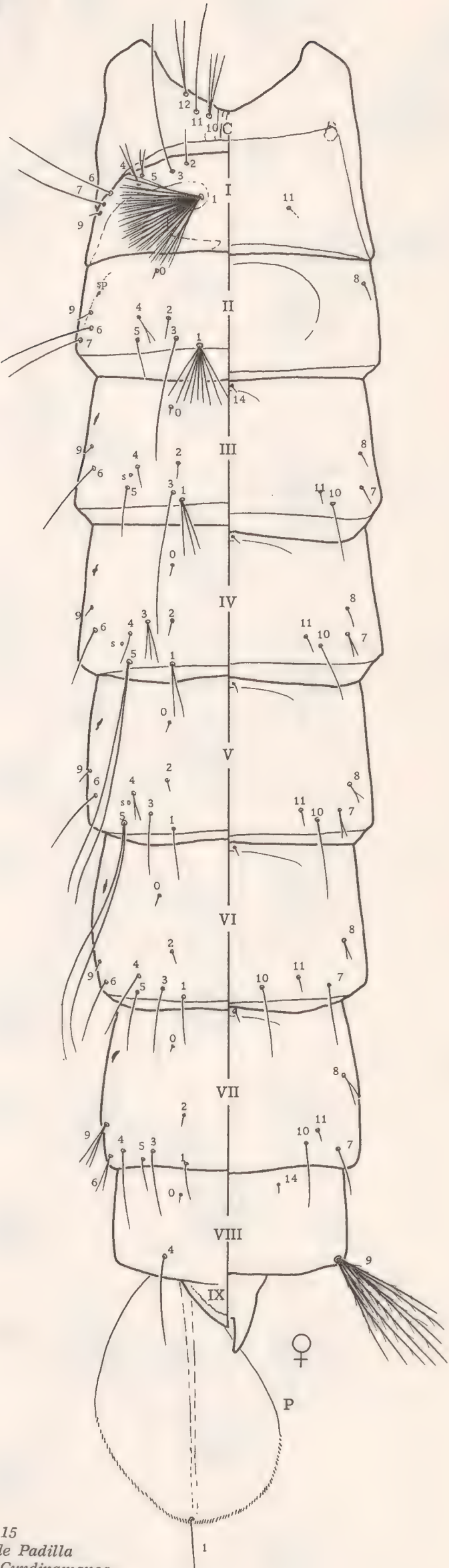
leei

HOWARDINA

Fig. 56



osornoi



COB 34-15
Chorro de Padilla
Bogota, Cundinamarca
Colombia

HOWARDINA

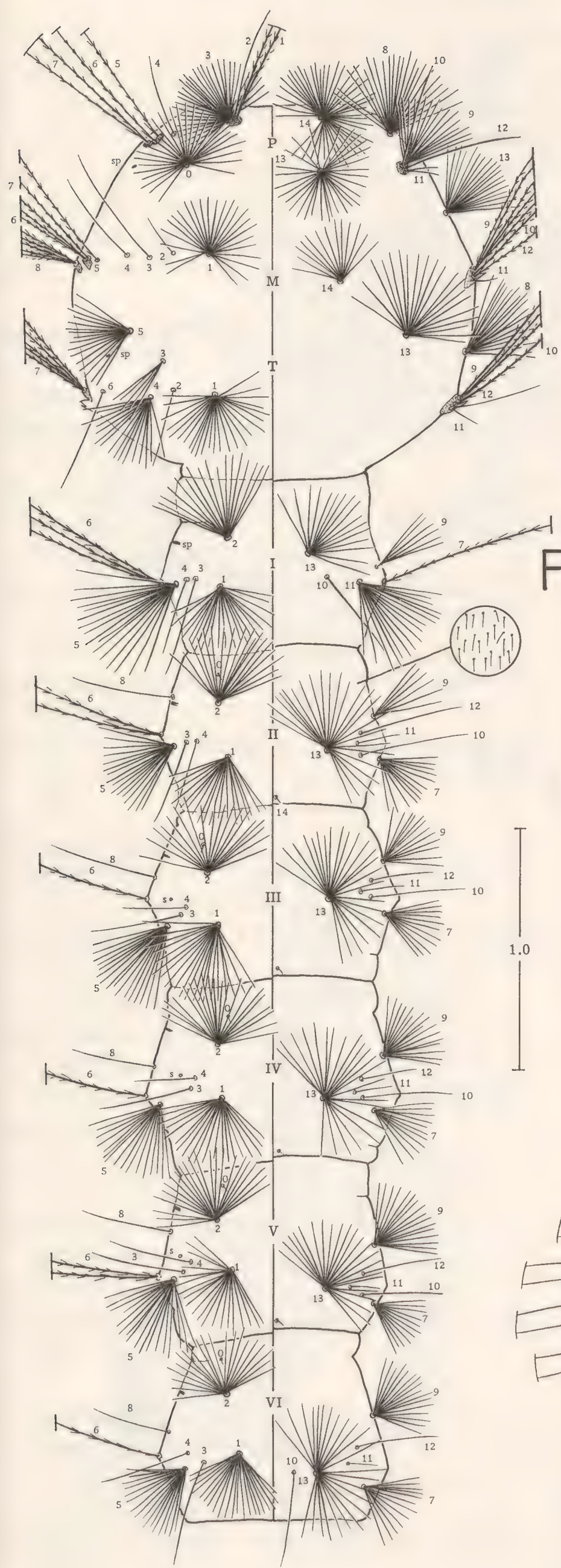
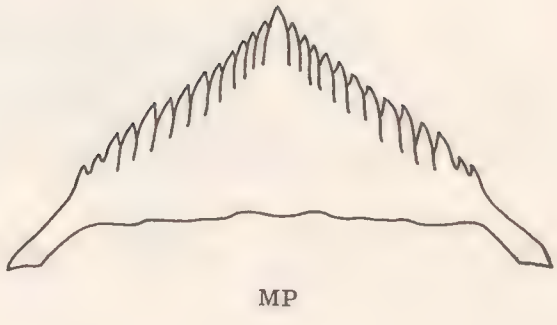
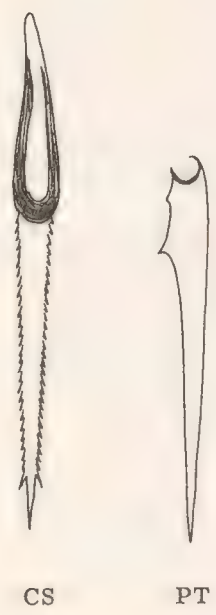
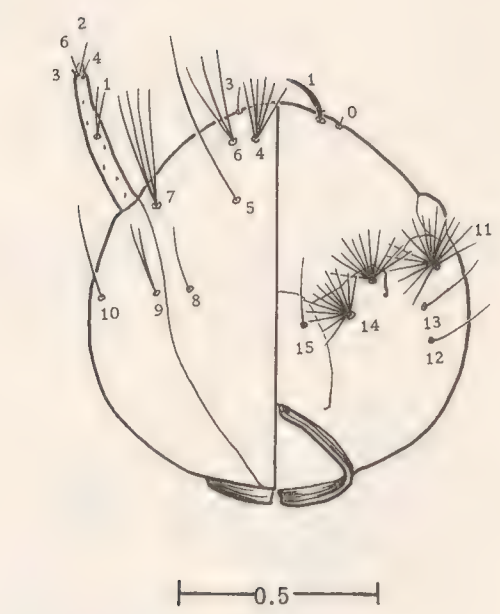
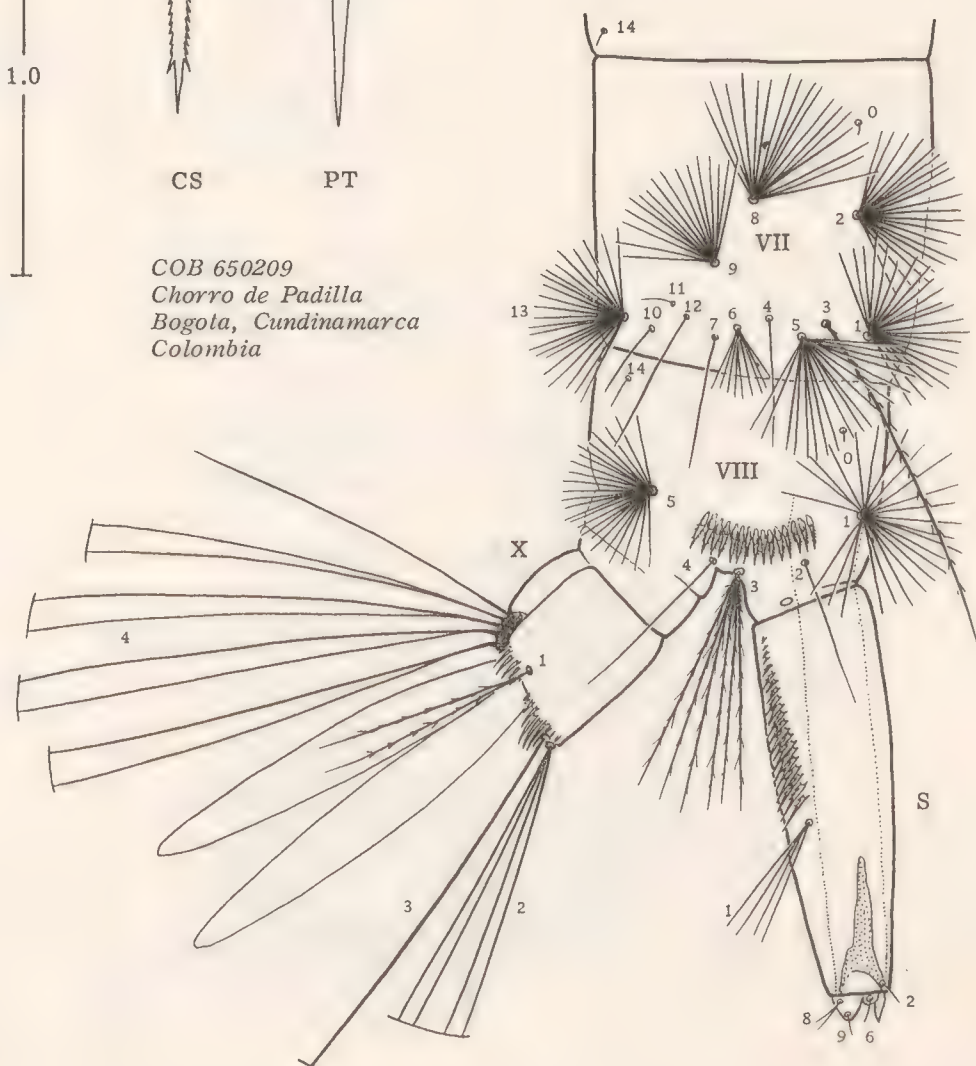


Fig. 57



COB 650209
Chorro de Padilla
Bogota, Cundinamarca
Colombia



osornoi

HOWARDINA

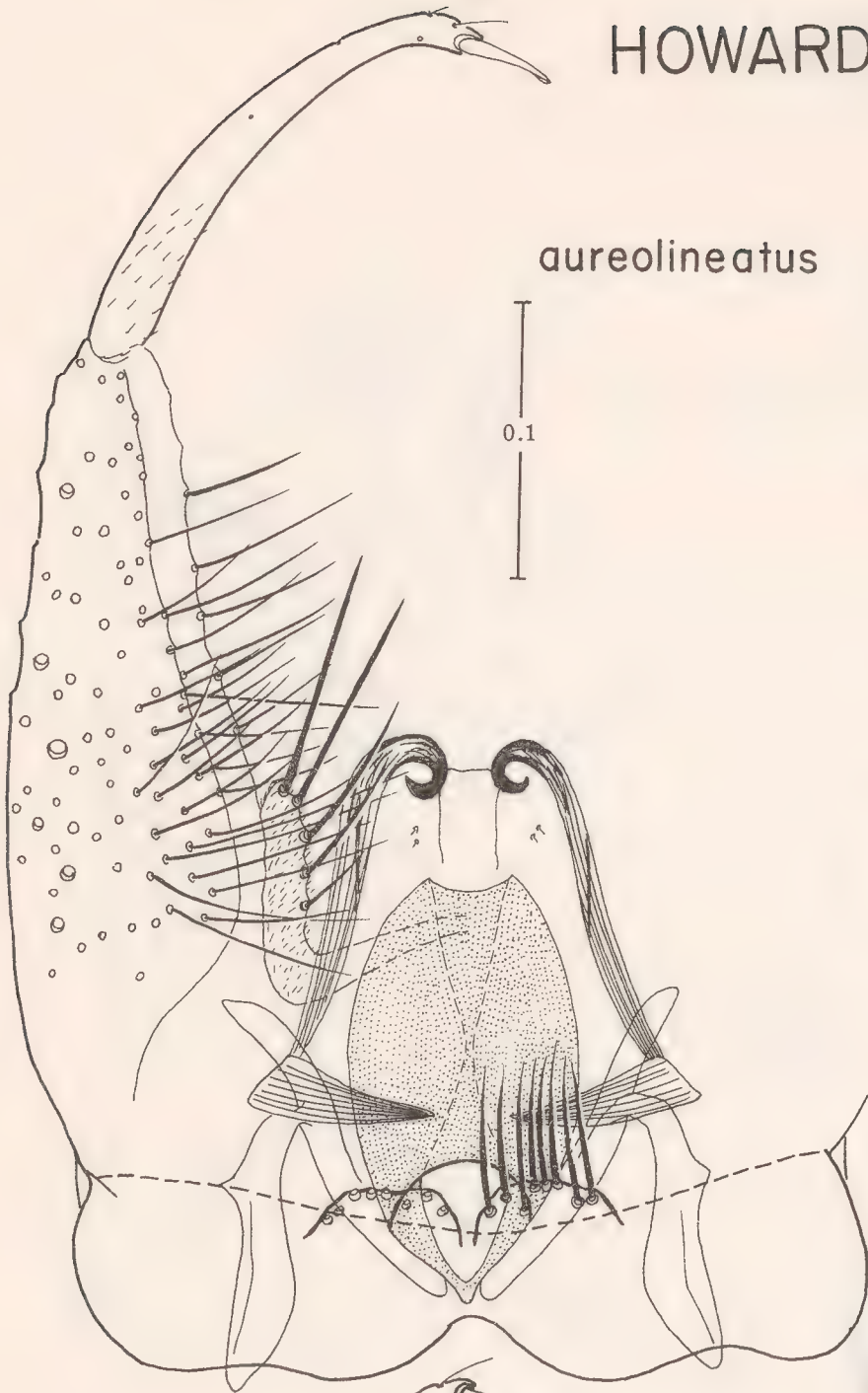
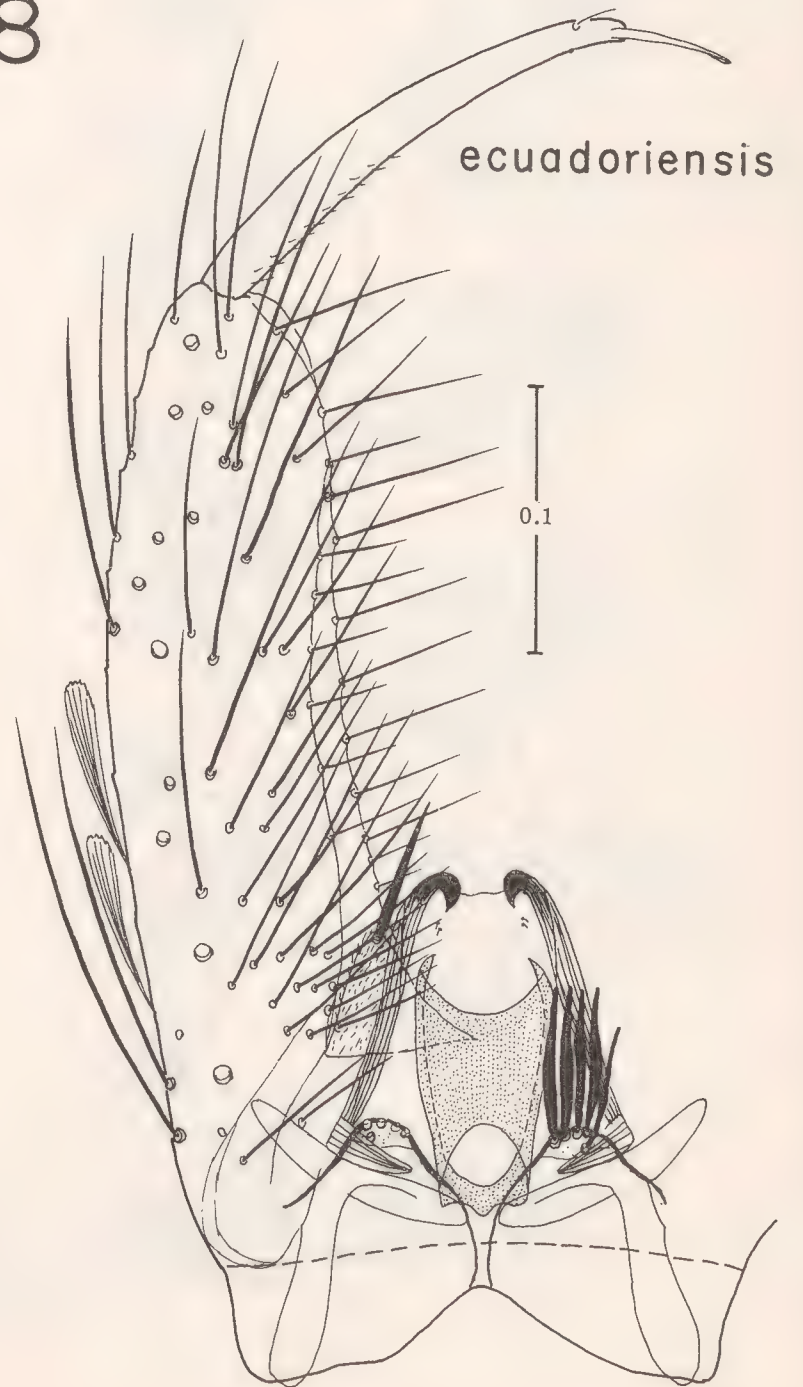
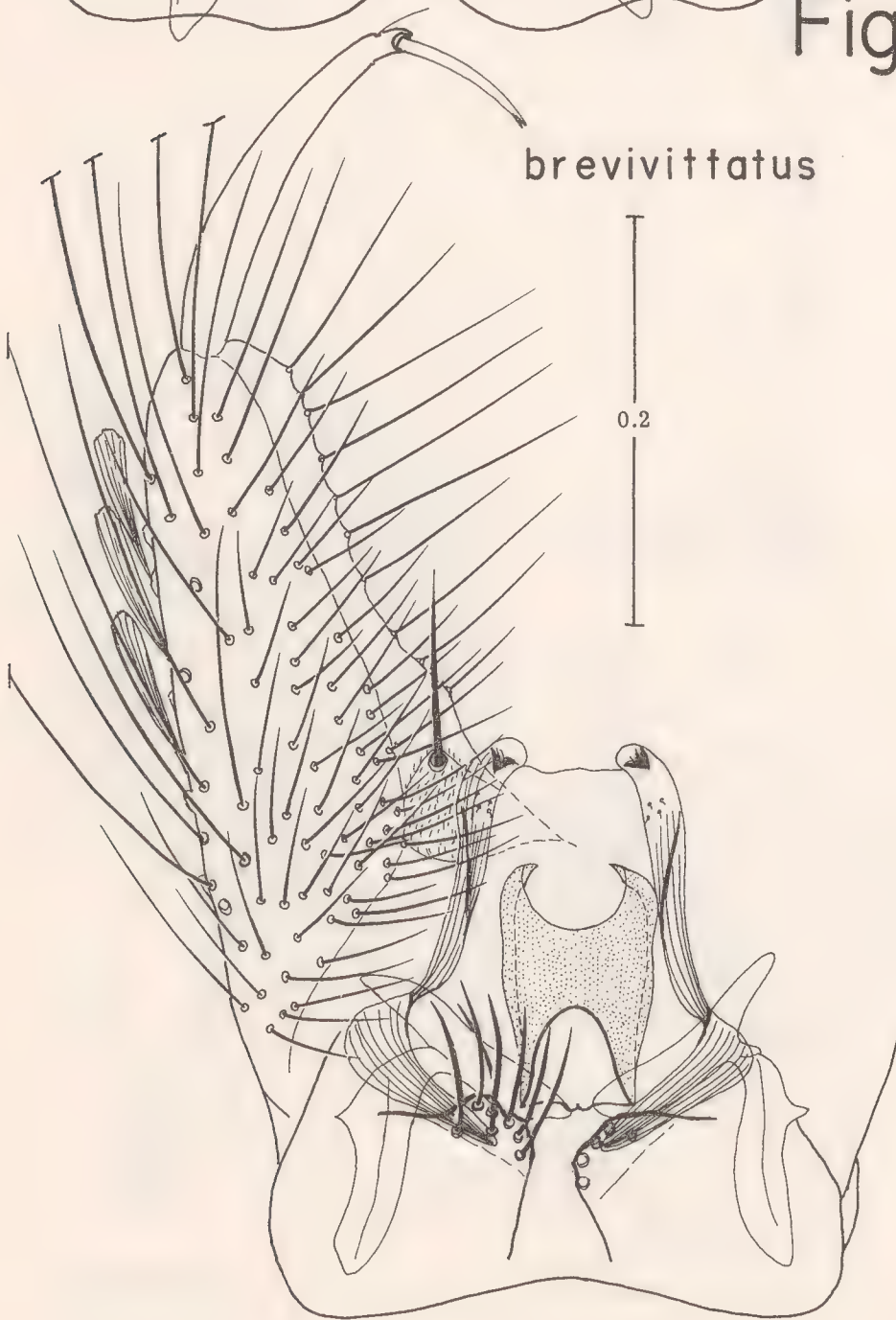


Fig. 58



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Names of valid taxa included in *Howardina* are in **boldface type**, names of valid extralimital taxa are in roman type. *Italic type* is used for names of all taxa considered invalid in this work (synonyms, homonyms, misidentifications, gross erroneous spellings, and so on). Misidentifications or invalid taxonomic interpretations are indicated by the use of the term "of authors" or "of" followed by a specific author, and are listed as separate entries following the entry for the correctly applied identical name.

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BIOLOGY, TAXONOMY, AND EVOLUTION
OF FOUR SYMPATRIC AGRILUS BEETLES

(COLEOPTERA: BUPRESTIDAE)

by

Robert W. Carlson

and

Fred B. Knight

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INTRODUCTION

Objectives

Beginning in the summer of 1964 we endeavored to study the natural history and taxonomy of four sympatric Agrilus Megerle¹ (Coleoptera: Buprestidae). These Agrilus were of particular interest because of their morphological similarities. Three of them, the bronze birch borer (Agrilus anxius Gory), the bronze poplar² borer (A. granulatus liragus Barter and Brown³) and the aspen root girdler (A. horni Kerremans) had only been distinguished rather recently. The fourth species, A. pensus Horn (= betulae Fisher) is distinct from the others in coloration, but very similar otherwise. The credibility of contentions that these taxa are very closely allied will be deliberated here in the light of:

1) A taxonomic study of these and related Agrilus, which included working both with specimens and literature.

2) An analysis of their larval habits, their ecological relationships to their hosts, and their population-limiting factors. Much of what is known about these aspects is taken from the literature and reinterpreted in the light of more recent findings, and pertinent writings on other Agrilus are also discussed.

3) Direct and indirect observations on the behavior of the adults in the field and laboratory.

4) A preliminary study of interspecific mating and a theoretical analysis of phylogeny, zoogeography, and speciation (or subspeciation).

Historic Background

THE BRONZE BIRCH BORER. A. anxius is probably the most notorious Nearctic species in the genus, and at one time was thought to be the cause of birch dieback. It was first recognized as a pest of shade trees and ornamental birches in the late 1800's and was called "the bronze birch borer" by Chittendon (1898). Chittendon says that "one correspondent has expressed the belief that if radical measures are not adopted, the loss of every birch in the city of Buffalo in the near future is imminent. This insect has already destroyed the common white birch [Betula papyrifera] and . . . many of the cut-leaf and European white birches. It even attacks trees planted but a year before."

Most of the reports of damage came from the northeastern U. S., perhaps because more birches had been planted there as shade trees. Nevertheless,

¹The majority of authors credit Curtis (1825) with originating the name Agrilus. However, Megerle (1823) published a price list in which the heading "Agrilus v. M. Buprestis)" appears. This simple listing credits Megerle with authorship, and Curtis (1825) merely designated one of Megerle's included species, Buprestis viridis L., as the genotype.

²The term poplar will here be used to refer to species in all sections of the genus Populus.

³Described as Agrilus liragus Barter and Brown (1949); status changed by Carlson (1969).

the problem was not confined to that region. Chittendon (1900), for example, notes that in 1899 "Prof. F. C. Newcombe of the University of Michigan, Ann Arbor, Mich., wrote that what was without doubt this species, and which he designated as the white birch borer, had been in that locality for two or three years and had killed half the white birches in the city of Ann Arbor."

Swaine (1918) first reported anxius killing trees in forests. This was the start of a devastating and puzzling epidemic of birch dieback which primarily affected Betula papyrifera, although some mortality of Betula lutea (= alleghaniensis) was also ascribed to this affliction. By 1951, 67 percent of the birches in Maine had been killed, and 15 percent of those remaining were in a decadent state due to the effects of birch dieback and bronze birch borer attack (Nash, Duda, and Gray, 1951).

Much research concerning the bronze birch borer and dieback in the 1940's and 1950's was directed at determining whether or not the beetle was causing the death of the trees. This question was hardly a new one then. Chittendon (1898) says "as in the case of injury ascribed to the two-lined chestnut borer [Agrilus bilineatus Weber] there is still a certain question of doubt as to whether or not this birch borer is really the primary cause of the death of the trees. Our correspondent is of the opinion that the injury in Buffalo is due primarily to the attack of this borer, since it has been observed attacking vigorous trees." The work of Anderson (1944), Nash et. al. (1951), and Barter (1957) shows, however, that the insect played a secondary role, usually killing those trees already afflicted with birch dieback. Whether or not birch dieback was the predisposing factor in earlier ravages of the bronze birch borer, when it allegedly killed mostly shade trees, is dependent upon what birch dieback really is. It is evident that the shade trees in many cities were in a weakened condition in the late 1800's, perhaps because of droughtiness.

THE BRONZE POPLAR BORER. The habits of A. granulatus liragus adults were first observed and recorded by Lintner (1883) before anything was published about the habits of A. anxius, and of course well in advance of the establishment of the fact that the poplar feeder and birch feeder were not one and the same. Chittendon (1898) says, "a very singular thing in connection with the occurrence of this borer in birch is that in spite of frequent search, extending over a period of two years, our correspondent has been unable to find this insect attacking any other tree than birch--a remarkable condition of affairs when we consider the numbers of observations by careful observers of its occurrence on poplar and willow."

Smith (1949a) discovered that the A. anxius (sensu Fisher, 1928) reared from Betula spp. had 22 chromosomes, while those reared from Populus spp. had only 20. Subsequently, Barter and Brown (1949) named the poplar feeding form A. liragus. Although A. granulatus liragus has habits nearly identical to those of anxius (host specificity excepted) it has never been accorded any great significance as a pest. Like anxius the bronze poplar borer attacks and kills only trees in weakened condition (Barter, 1965). because poplars are used less frequently as ornamentals than birches, g. liragus is not as important an ornamental pest as anxius. Furthermore, no large scale maladies on the order of birch dieback occur in forests of native North American Populus spp. so that the bronze poplar borer has not been associated with forest devastation.

THE ASPEN ROOT GIRDLER. Harrison (1959) discovered what he thought to be a new species of Agrilus feeding on the roots of aspen suckers (Populus tremu-

loides and P. grandidentata). The establishment of a chromosome number of 22 for this species seemed to indicate that it was more closely allied to anxius than to g. liragus (Nord, 1962). Later, Nord, Knight and Vogt (1965) discovered that the proper name for the root boring form is A. horni, a name which Fisher (1928) and Barter and Brown (1949) thought to be a synonym of anxius. Because of their uncertainty, however, they did not synonymize horni with anxius.

A. horni has attained a modest reputation as a pest. Nord (1962) says that it caused severe damage to hybrid aspen out-plantings which were part of genetics experiments conducted by the Institute of Paper Chemistry in Wisconsin and Michigan. In 1964, the trees in some of the affected plots were destroyed and the tests were reinitiated. However, in 1964 they were still having trouble controlling horni.¹ This, no doubt, was due to the inappropriateness of the control techniques used, rather than to any factor in the beetle's ecology which makes it difficult to control. Moreover, because of its ecological preferences, it is not likely that this insect will ever cause great injury to well-stocked natural stands of aspen suckers that are growing on areas of moderate or good site quality.

THE ALDER-BIRCH BORER. Fisher (1928) was uncertain of the status of A. pensus. He says "this species may only represent a color variety of anxius, but since nothing is known of its habits, it is best to retain it for the present, at least, as a valid species." Even though he was unsure of the distinction between pensus and anxius, he took the liberty of describing betulae, a synonym of pensus, from 3 specimens. Although there is really little question that pensus is actually a distinct species, its biology remained almost unknown prior to the studies here described. The ecology of pensus makes it rather innocuous, and it has attracted little attention. However, it appears to be an important factor in the ecology of alders (Alnus spp.), which are important as wildlife cover in their lakeside and streamside habitat.

TAXONOMY

The Genus Agrilus

SIZE AND DISTRIBUTION. Agrilus beetles are thought to feed only on angiosperms (Fisher, 1928). Confinement to angiosperms could indicate that the genus arose in the Cretaceous or later, which seems to allow ample time for it to have attained the vast size and worldwide distribution it presently has. Schaefer (1949) said the genus included 2500 described species, and Obenberger (1957) claimed that in his collection alone, there were over 3000 described and undescribed forms. Obenberger (1959) believed that there are over 4000 species of Agrilus.

The largest number of species occur in tropical or subtropical areas, but Agrilus is well-represented in temperate regions too. Fisher (1928) recognized 125 described forms from the North American fauna (North of Mexico), and a considerable number have been described since, mostly from the south-

¹Personal communication, 1964; D. Einspahr, Institute of Paper Chemistry, Rhinlander, Wisconsin.

western United States.

SUBDIVISIONS. Obenberger (1957, 1959), with some rather specious reasoning, tried to show that there is no way to divide Agrilus into acceptable subgenera. He was, however, willing to admit that there are some recognizable species groups.

The economically important Eurasian "species"¹ Agrilus viridis L., its many destructive "host races," and the lesser known North American A. politus Say together represent such a species group which is extremely difficult taxonomically. Both A. politus and A. arcuatus Say are classified by Fisher (1928) as being composed of several sympatric "subspecies," but each actually represents a multi-species "complex."

Frost (1912) recognized some of these "sibling species" problems, and presented suggestions for their solution. He concluded by saying "the studies in the otiosus² and anxius groups have been so far, rather disappointing, due to the difficulty of getting series of both sexes. The only species that is at all abundant in this locality is otiosus, taken on oak leaves. The olivaceous variety of acutipennis has been encountered quite often on oak, and bilineatus occurs in favorable places on oak sprouts, but in general the species turn up singly or in pairs, with aggravating slowness. Several very interesting problems are suggested by the material in hand, and more specimens from widely separated areas may present a solution." In many groups of Agrilus, a similar situation still exists.

The Agrilus anxius Group

DEFINITION. Presumably broadening the limits of the Agrilus anxius group sensu Frost (1912), it is here defined as those species in which the adults have the carina of the pygidium projecting as a spine, (figs. 2, 3), and (2) have a sexual dimorphism in the structure of the last abdominal segment. The marginal sclerite³ of the hind segment is smooth and in males lies in a plane nearly confluent with that formed by the sternite (fig. 33). In females the marginal sclerite is reflexed or beveled with respect to the sternite (fig. 32). In most of the species the first and/or second abdominal sternites are also sexually dimorphic. In males these sternites are often grooved medially (fig. 1), while females never have such a groove.

NOMENCLATURE Nord et al. (1965) have referred to the "Agrilus anxius complex." The term complex carries a connotation of propinquity that is inappropriate for a group that includes anxius, g. liragus, and horni, and we,

¹Actually includes a number of sympatric species (see, for example, Basurmanova, 1958).

²Agrilus otiosus Say.

³Those parts of the tergites termed the "vertical portions of the segments" by Fisher (1928), but they are not vertical on the hind segments and the term marginal sclerite seems to be a preferable alternative.

therefore, will not apply it here. The Agrilus anxius group is comparable to what in many other families of insects would be recognized as a genus. Were the anxius group to be delineated from other Agrilus as either a subgenus or genus, either of the Agrilus synonyms Teres Harris (1829) or Uragrilus Semenov (1935) (= Epinagrilus Stepanov, 1954) could be applied. Because the limits of the anxius group are not ascertainable from the literature, it would be unwise to use a formal name for it at this time.

MORPHOLOGIC ANALYSIS . The taxonomic analysis of anxius group species is based primarily on adult morphology, but important information is also furnished by other developmental stages. The interpretation of morphologic characters is strongly influenced by studies of adult behavior which are discussed later, and some findings from studies of adult morphology are deferred to the Evolution section.

Adults. The analysis of adult morphology was based primarily on collections made in Michigan (Iron, Gogebic, Benzie, and Manistee Counties) and Wisconsin (Vilas Co.). Material in the collections of the University of Michigan Museum of Zoology (Ann Arbor, Michigan) the Entomology Research Institute of Canada (Ottawa, Ontario), Harvard University, Museum of Comparative Zoology (Cambridge, Massachusetts), the Philadelphia Academy of Sciences (Philadelphia, Pennsylvania) and the U. S. National Museum (Washington, D.C.) was also examined. The following types were studied: Agrilus betulae Fisher, Agrilus fulminans Fisher, Agrilus populi Fisher, Agrilus horni Kerremans (= blanchardi Horn, name preoccupied), Agrilus nevadensis Horn, Agrilus niveiventris Horn, Agrilus pensus Horn, and Agrilus gravis Leconte.

On the basis of the study of the types and other material the following nomenclatural changes (including those made by Carlson [1969]) were called for and will be followed here:

AGRILUS BROWNI, new species

Agrilus browni, new species

Agrilus lateralis, sensu Fisher (1928), in part.



Fig. 1. Ventral aspect of Agrilus horni ♂, showing the median groove on abdominal sternites 1 and 2.

AGRILUS GRANULATUS Say

Agrilus granulatus granulatus SayBuprestis granulata Say (1823)Agrilus granulatus populi Fisher; status assigned by Carlson (1969)Agrilus populi Fisher (1928)Agrilus trichocarpae Chamberlin (1929)Agrilus granulatus liragus Barter and Brown; status assigned by Carlson (1969)Agrilus liragus Barter and Brown (1949)

AGRILUS PENSUS Horn

Agrilus pensus Horn (1891)Agrilus betulae Fisher (1928); synonymy designated by Carlson (1969)

AGRILUS QUADRIGUTTATUS Gory

Agrilus quadriguttatus quadriguttatus GoryAgrilus quadriguttatus Dejean (1833, 1836), nomen nudumAgrilus quadriguttatus Gory (1841)Agrilus quadriguttatus niveiventris Horn; status assigned by Carlson (1969)Agrilus niveiventris Horn (1891)Agrilus nevadensis Horn (1891); synonymy designated by Carlson (1969)Agrilus quadriguttatus fulminans Fisher; status assigned by Carlson (1969)Agrilus fulminans Fisher (1928)

AGRILUS RUFICOLLIS Fabricius

Agrilus ruficollis FabriciusBuprestis ruficollis Fabricius (1787)Agrilus lateralis Say (1823), new synonymyAgrilus sayi Saunders (1871), name unnecessary (lateralis not preoccupied)

Fisher (1922) reared an Agrilus sp. from bayberry (Myrica pensylvanica, = carolinensis) at Lyme, Connecticut, for which he used the name A. lateralis Say. The original description¹ of lateralis (Say, 1823), however, fits A. ruficollis Fabricius more closely than the species that was reared from Myrica. For that reason and because of the range limits apparent for it, the species which Fisher reared from Myrica is here given the name Agrilus browni n. sp.

Say (1823) says the head of lateralis has a profoundly impressed line, which certainly is characteristic of ruficollis. A. browni has the front only weakly impressed. Say also notes that the length of lateralis is 1/5 inch (about 5.1 mm), which is not exceptionally short for ruficollis, a smaller and more variable species than browni. On the other hand, specimens of browni as short as 5.1 mm must be extremely rare, as we have seen none approaching that size.

¹According to Fisher (1928) the lateralis type was lost, but, presumably, it was destroyed, as is the case for the majority of Say's specimens.

The only bonafide records for browni are from places very remote from the lateralis type locality. Say (1823) described lateralis from a specimen collected in Missouri, which then included the vast region west of the Mississippi known as the Louisiana Purchase, excluding what is now the state of Louisiana. Knull (1922) found browni in abundance on sweet ferns (Myrica asplenifolia, = Comptonia peregrina) in Pennsylvania, but no reliable records are known to us for any area west of that state. In spite of the examination of large amounts of sweet fern by P. C. Kennedy¹ and a modest amount of searching on that host plant by us, browni has not been encountered in Michigan. The strength of all the evidence leads us to suppress lateralis as a synonym of ruficollis.

Fisher (1928) provides a good description of browni (under the name lateralis), and his "lateralis" neotype² is here designated as the type of browni. The species is named for Mr. William J. Brown³, who suggested that Fisher (1922, 1928) had misapplied the name lateralis.

Fisher (1928) knew A. nevadensis Horn only from the type, and that specimen appears to have been deformed during pupal development. Fisher (1928) says its scutellum is not carinate, but the carina appears to be present, although it is positioned abnormally on the deformed scutellum. The somewhat prolonged elytra have more sharply pointed apices and more coarsely rugulose surfaces than typical q. niveiventris, but there are no other structural differences. The pigmentation of some specimens of q. niveiventris from southern California is as dark as that of the A. nevadensis type, which was collected in Nevada.

The following sections will be devoted primarily to anxius, pensus, horni, and g. liragus. The discussion of other members of the anxius group is deferred to a later section on evolution.

Since Gory (1841) described anxius, other forms have been named, two of which are synonyms, while another was mistaken for a synonym. Agrilus gravis Leconte and A. torpidus Leconte were described in 1859, but Fisher (1928) placed them as synonyms of anxius. Agrilus blanchardi Horn (not Saunders) and A. pensus Horn were described in 1891. Because the former was a primary homonym, it was renamed A. horni by Kerremans (1900). Fisher (1928) thought that horni was a synonym of anxius. Knowing of no material besides the type which could be identified as horni, he believed that it was merely an abnormal specimen. Being somewhat uncertain, however, he retained horni as valid.

When Barter and Brown (1949) established that a poplar-feeding form and a birch-feeding form had been confused under the name anxius, they decided

¹Personal communication, 1967; P. C. Kennedy, North Central Forest Experiment Station, U. S. Forest Service, East Lansing, Michigan.

²According to Fisher (1928), this specimen is a male, which he collected on bayberry at Lyme, Connecticut and deposited in the U. S. National Museum collection.

³Entomology Research Institute, Canada Department of Agriculture, Ottawa, Ontario.

to retain¹ that name for the birch-feeding form. They suppressed torpidus as a synonym of anxius, but made no definite decision regarding the name gravis. The gravis type is a female that Barter and Brown (1949) could not identify reliably. The name liragus was, therefore, given to the poplar feeding form with the distinct possibility of it later proving to be a synonym of gravis. There have been doubts that this was the proper thing to do. For example, the application of gravis by Blanchard (1889) for the species collected on poplars (not "sprouts"²) is cited by Nash et al. (1951) as a possible indication that gravis was the proper name for the poplar feeder.

Although the gravis type lacks the coppery sheen often found on the head and pronotum of anxius specimens, its absence is not a good indication of the identity of the type. Vogt³ pointed out that specimens of anxius from some parts of the Great Lakes Region are often colored more like g. liragus than are specimens from more eastern parts of the United States. Indeed, the coppery reflections are often very indistinct in specimens from the Upper Peninsula of Michigan, which lies within the type locality recorded by Leconte (1859) as the "Lake Superior Region."

By relying on characteristics other than coloration and working with specimens collected in the Upper Peninsula of Michigan, we found that Agrilus gravis Leconte is really a synonym of anxius Gory, and therefore g. liragus Barter and Brown is to be retained as valid. The name gravis, as used in a number of papers in the late 1800's, refers to either anxius or g. liragus; assignment to one or the other depends upon the host designated, if any. References using the other anxius synonym, torpidus Leconte, are to be treated similarly, except for those which refer to willow as a host. The latter (e.g. Cook, 1890; Davis, 1891, 1892) refer to A. criddlei Frost, which makes galls on willows. The host of criddlei was recently established through rearing by Wong and McLeod (1965).

Barter and Brown (1949) concluded that anxius and g. liragus are separable only by reliance on male genitalia, coloration of the head and pronotum, and host plant identity. We cannot concur with them fully. As previously indicated, anxius specimens from some areas do not have very distinct coppery reflections on the pronotum, and this iridescence also seems to fade quite rapidly in some museum specimens. Wetting the specimens with various relaxing agents is particularly destructive to the iridescence of these beetles. On the other hand, there are structural differences, besides male genitalic ones which, in combination, can be used for separating anxius and g. liragus. One of these, a difference in the form of the tarsal claws, was not noted by Barter and Brown (1949). The membraneous attachment of the tarsal claws of g. liragus appears to be either more flexible or looser than that of anxius. Consequently, the g. liragus tarsal claws are often clearly separated from the unguifer, making the

¹They indicated the location of the anxius type as being unknown.

²Blanchard thought what he had found on poplar sprouts was anxius.

³Personal communication, 1966; G. B. Vogt, U. S. Dept. Agr., A.R.S., Entomology Res. Div., Washington, D. C.

latter clearly visible. The claws of anxius are attached so that there is very little space between their bases and the unguifer. The unguifer, is therefore, more difficult to see. In addition, the claws of anxius are usually rather distinctly swollen at their bases, and tend to obscure their attaching membrane which stretches across the opening in the last tarsomere, while in g. liragus the basal parts of the claws are usually not strongly swollen, and the membrane in the tarsomere opening is usually readily visible.

The females of anxius and g. liragus differ in the shape of the projecting spine on the pygidium, but the males do not. In g. liragus females the spine usually projects strongly (fig. 2) and is rather cylindrical, while in anxius females it is usually shorter and more blunt (fig. 3), and its tip is often broad and elliptical in end view.

A useful characteristic mentioned by Barter and Brown (1949), is the tendency for the elytral tips of g. liragus to be acute and strongly serrate (fig.

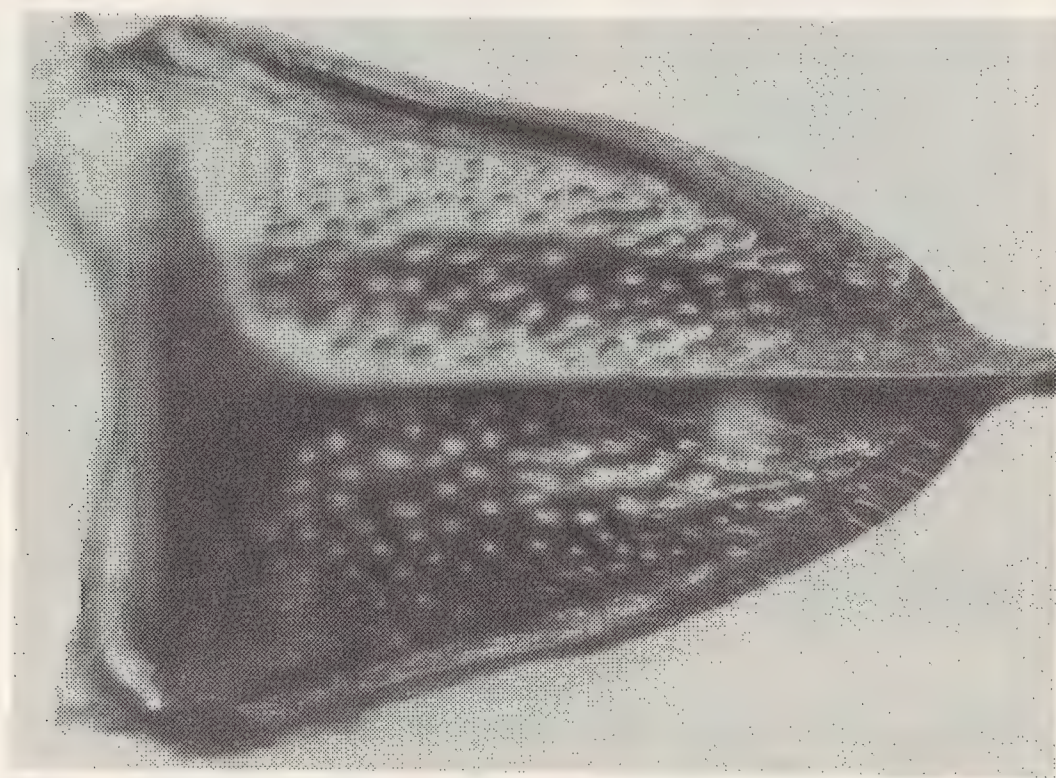


Fig. 2. Dorsal surface of the pygidium of an Agrilus granulatus liragus ♀ (X40).

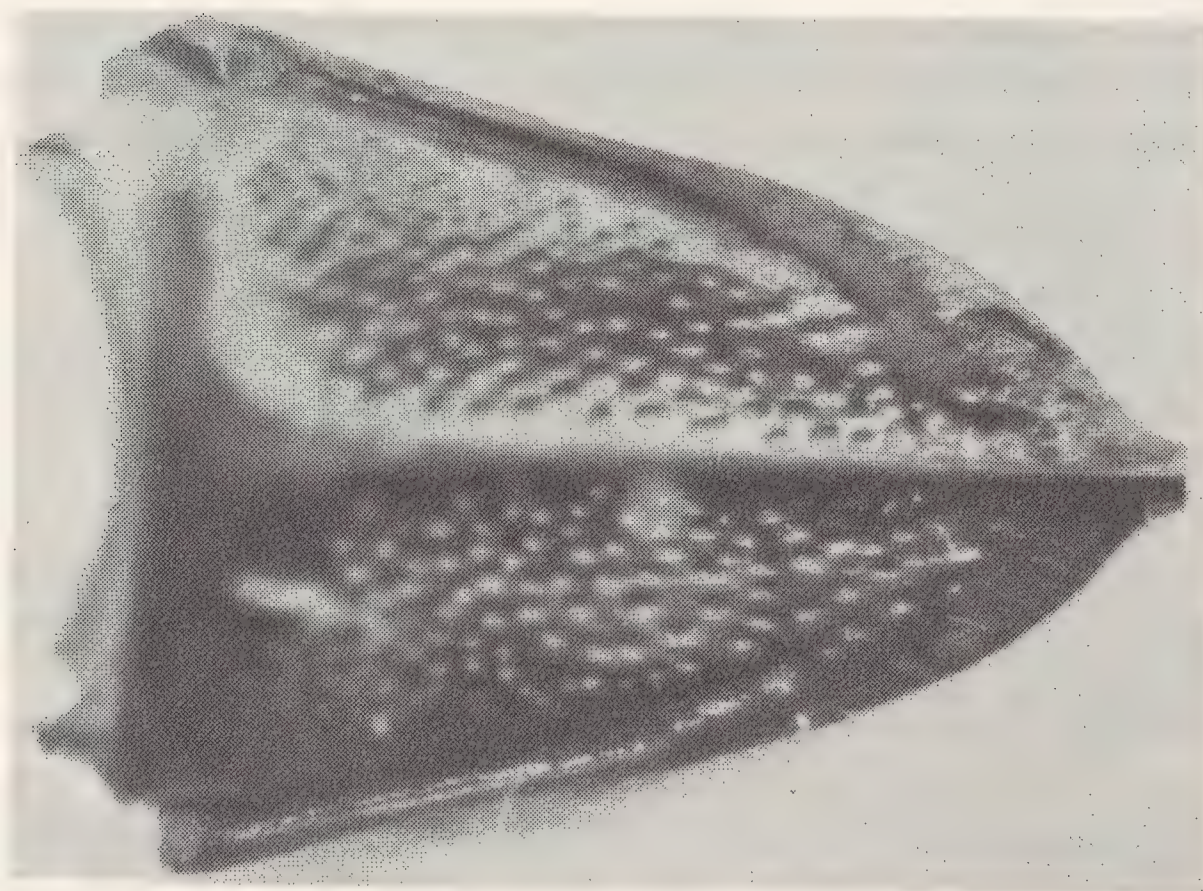


Fig. 3. Dorsal surface of the pygidium of an Agrilus anxius ♀ (X40).

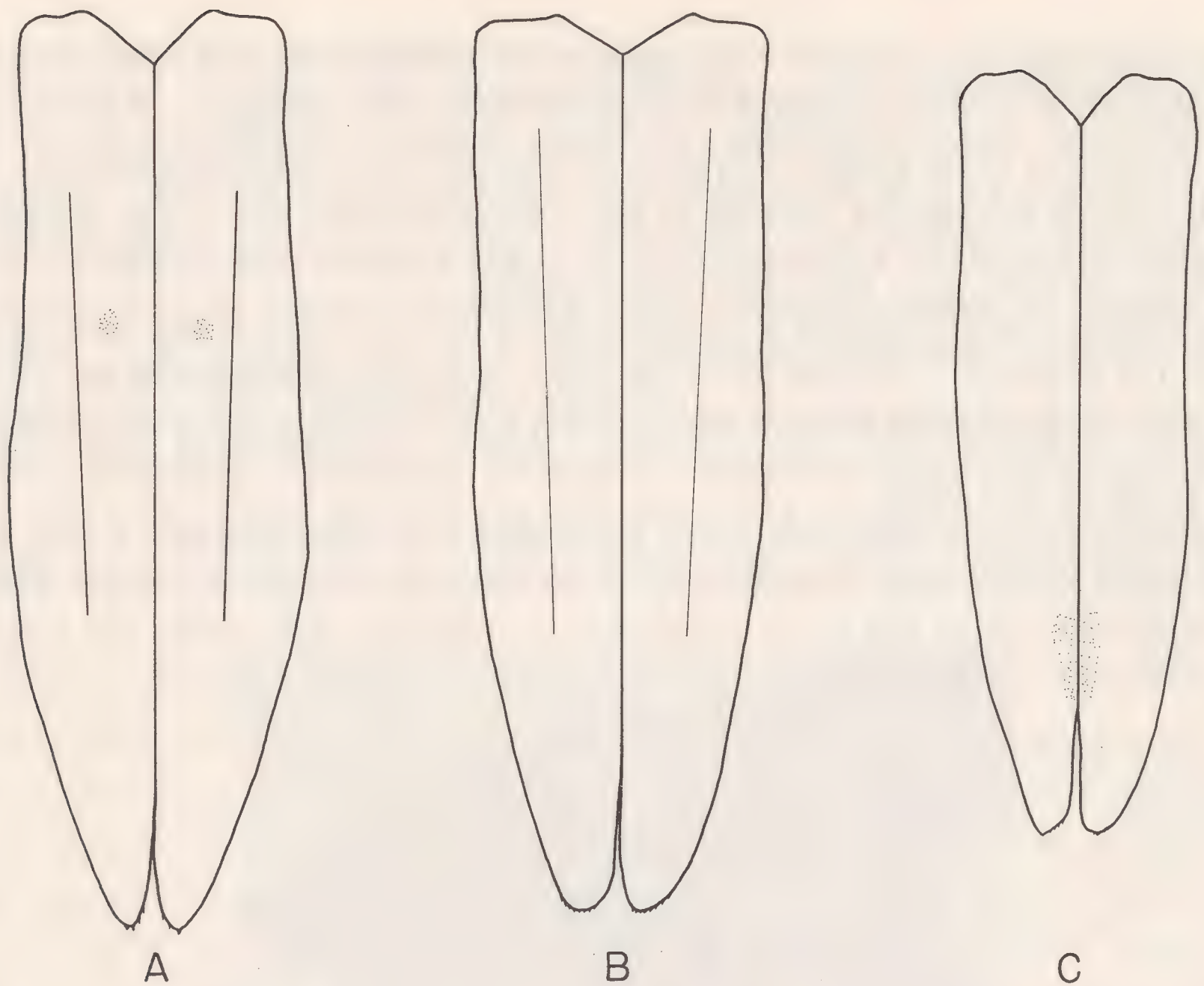


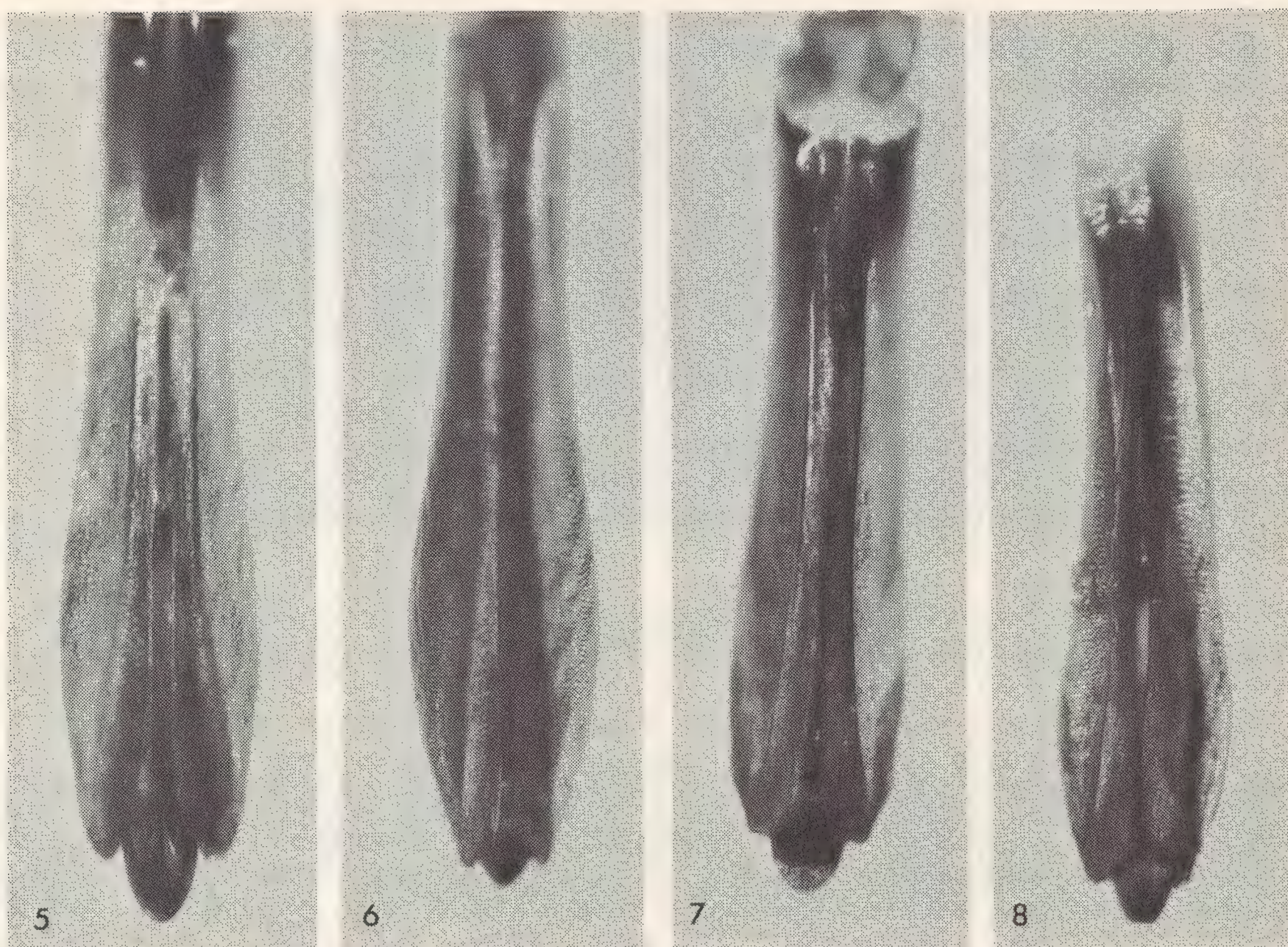
Fig. 4. Elytra of A. granulatus liragus ♂ (A), A. anxius ♀ (B), and A. pensus ♂ (C).

4a), while those of anxius are more broadly rounded and not as strongly toothed (fig. 4b). By using both the coloration differences and the somewhat obscure and somewhat variable structural differences of the pygidial spine, tarsal claws, and elytra it is usually possible to distinguish the females of anxius and g. liragus.

The most reliable characters for separating males of anxius and g. liragus are those of the aedeagus. The parameres of anxius have broad ventral inner margins, and these margins together form a trough which is broad and shallow (fig. 5). Ventrally, the inner margins of the g. liragus parameres are usually narrow, together forming a trough which is narrow but deep in comparison with that of anxius (fig. 6).

Nord et al. (1965) separate horni from anxius and g. liragus by utilizing characteristics of both the male and female genitalia. The ovipositor of horni (relative to elytron length) is significantly shorter than that of g. liragus or anxius. Nord et al. also pointed out that the average ovipositor length is less in g. liragus than in anxius, and in some cases the minimum length for g. liragus approaches the horni maximum. However, they found no overlap in ovipositor length between g. liragus and horni.

The male genitalia of these species correspond in length to those of the females. In addition to being shorter, the aedeagus of horni differs from those of anxius and g. liragus in having parameres which are less dilated posteriorly, their margins being subparallel (fig. 7). Nord et al. (1965) say that ventrally and subapically the inner margins of horni parameres are arcuate to subarcuate, while those of anxius and g. liragus are angulate to subangulate.

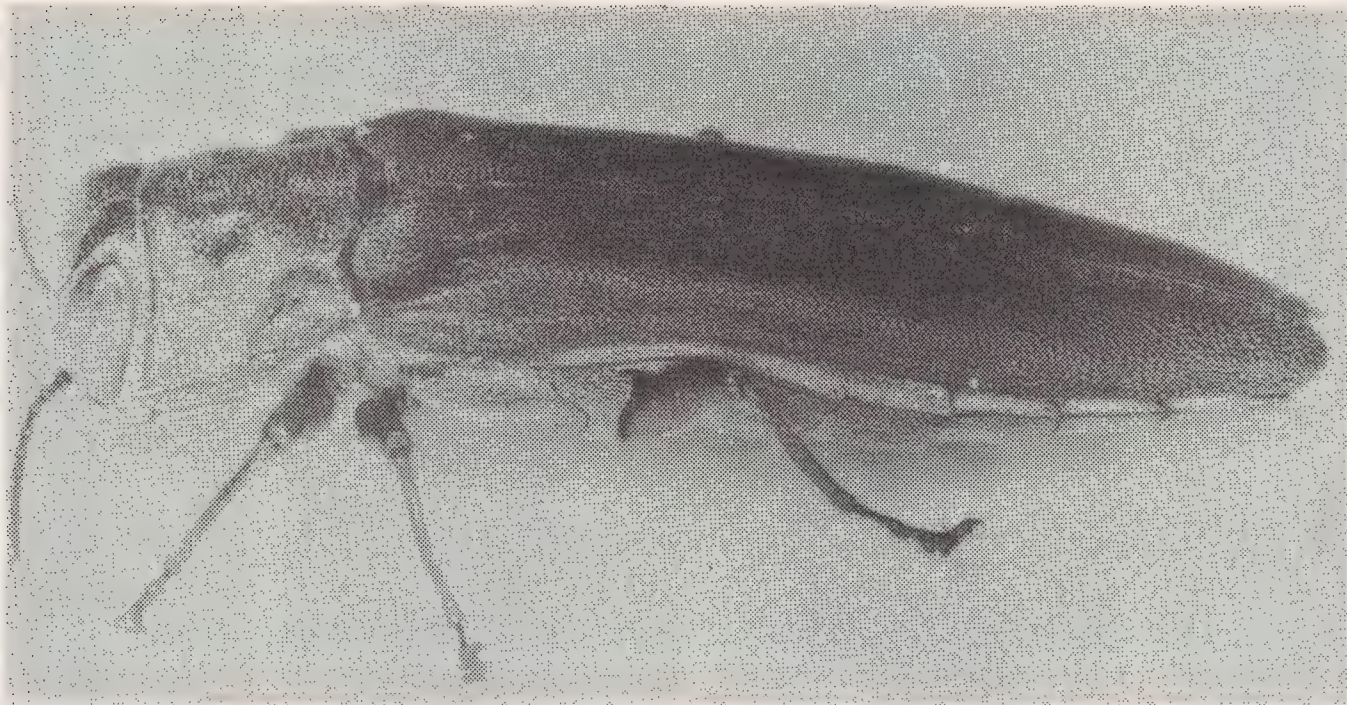


Figs. 5-8. Ventral sides of the aedeagi of Agrilus anxius (5), A. granulatus liragus (6), A. horni (7), and A. pensus (8).

The ventral trough formed by the parameres tends to be intermediate in form to the troughs of anxius and g. liragus, which are quite different from each other.

Despite the confusion which has occurred regarding the identity of horni, it is really quite distinct from either anxius or g. liragus. Besides the genitalic differences already noted, horni differs significantly from anxius and g. liragus in other ways. Most significant of all, perhaps, is the moderately dense pubescence on the marginal sclerites of the abdomen. As Horn (1891) points out, this pubescence appears all the more distinct because of the white pruinosity which is associated with it. Together, the pruinosity and white pubescence tend to form a white band which is very distinct on newly-collected horni specimens, but also quite noticeable on material that has been preserved for many years. The pubescence is usually dense enough to obscure the sculpturing of all the marginal sclerites, except for the last one. These marginal sclerites are usually less pubescent in anxius and g. liragus, and the pubescence is usually not dense enough to obscure the sculpturing of the marginal sclerites. Moreover, the marginal sclerite of the second abdominal segment is either glabrous or noticeably less pubescent than those of the first and third segments in anxius and g. liragus.

There are also distinct differences in the structure of the elytra. The texture of horni elytra is very even, the disc being comparatively smooth, finely imbricate, and usually lacking a distinct longitudinal costa (fig. 9). The disc is usually more coarsely imbricate in anxius and g. liragus, and often has a

Fig. 9. *Agrilus horni* ♂.

longitudinal costa and a rather distinct depression just mesad of the costa and between the disc's basal third and apical half. Frequently in *g. liragus*, and sometimes also in *anxius* (see ♂, fig. 39), this depression is pruinose, the pruinosity forming a spot similar those on the elytra of *g. granulatus*, but less distinct. Upon close examination, the parts of the depression where the spot tends to form can usually be seen to have a small group of recumbent hairs which are aligned differently and sometimes longer than the surrounding ones. The pruinosity usually disappears in preserved specimens, but the faint spot formed by the unaligned hairs can often be detected.

The recumbent pubescence on the elytra of *horni* is distributed rather evenly over the surface and is also rather short and uniform in length. That of *anxius* and *g. liragus* is usually not uniform in distribution or length, and many of the hairs are longer than those of *horni* elytra.

The structure of the head is also somewhat different in *horni*. The front is almost always rather flattened in profile. Sometimes in *anxius* and even less frequently in *g. liragus*, the front is somewhat flattened in profile, but in these species it usually bulges, presenting a rounded profile.

The form of *Agrilus pensus* is intermediate between that of *A. anxius* and *A. quadriguttatus* Gory, the latter being a willow feeding species. Barter and Brown (1949) say that the male genitalia of *pensus* are structured like those of *g. liragus* and *g. populi*, but this is not true. The *pensus* aedeagus (fig. 8) is somewhat variable, but more like that of *anxius* than that of *g. liragus* or *g. populi*. Barter and Brown also say that *pensus* lacks pubescent and pruinose spots on the elytra, but while they are not found on specimens from Nova Scotia and New Brunswick they are quite apparent on some specimens from Michigan and are also found on the type of the *pensus* synonym *betulae* Fisher. As in *A. quadriguttatus* and subspecies the subapical maculation of the elytra is likely to be spread out along the elytral suture instead of concentrated in a small spot. Also as in *A. quadriguttatus* the elytra are likely to be angulate at the apex (fig. 4c), forming a broad notch, instead of acuminate as in *A. granulatus* and subspecies, which have a narrower notch between the apices.

Eggs. The eggs of *pensus* (Engel, 1968), *anxius*, *g. liragus*, and *horni* are creamy white immediately after they are deposited. They are flattened and

oval in outline. There seem to be no interspecific differences in egg size, those of horni being about 1.2 mm long by 0.8 mm wide, according to Nord (1962).

The eggs of anxius (and presumably g. liragus) are coated with a semi-transparent whitish substance immediately following deposition (Barter, 1957). The substance apparently acts as a cement and as a protectant for the soft egg shell. There is no evidence that horni applies such a substance to its eggs. Instead, the chorion of horni eggs appears to toughen as the larvae develop, and as a result they turn dark brown to black. The eggs of anxius and g. liragus darken like this only when parasitized. They develop grayish-black streaks and then become completely black prior to emergence of the parasite adult (cf Barter, 1957, 1965). This led Nord et al. (1965) to believe that the darkening of horni eggs may have been associated with parasitism, but this is not the case.

Larvae. Benoit (1965) presents a complete description of g. liragus larvae, and gives the differences between these and the larvae of anxius. He says the larvae of these species are about 30 to 40 mm long and 2 to 3.5 mm wide¹. The body is white, except for the anal forceps and other minor sclerotized portions, which are ferruginous. The prothorax, which is wider than the rest of the body, has a median I-shaped sclerotized line on the tergum. A similar structure, which is only vaguely sclerotized, is located on the prosternum (Barter, 1957). The segments posterior to the prothorax are all about equal in width.

Benoit (1965) says C-shaped spiracles are located on abdominal segments one through eight, and similar, but somewhat larger ones are found dorsolaterally on the mesothorax. Actually, the sclerotized C-shaped structure is part of the spiracular valve, and the spiracular opening itself is located internal to the transparent valve.

Benoit (1965) states that the labial palpi are absent, but this is not true. Apparently he missed them because they were out of focus when his microscope was focused on the rest of labium (cf fig. 10 and his fig. 1B).

Because of the nature of his samples, Benoit's morphologic comparison of the larvae of anxius and g. liragus is of questionable value. He obtained his material from two localities, one for each species. This could hardly give one an adequate sample of intraspecific variation.

Nevertheless, the species differences in the coloration of the anal forceps which Benoit has listed do appear to hold for larvae collected in Michigan as well as for those from Quebec. The anal forceps of anxius are described by Benoit (1965) as being reddish, with the line of sclerotization extending anteriorly beyond the anal opening. He says the forceps of g. liragus are more brownish, with the sclerotization ending abruptly just posterior to the anal opening. The larvae of pensus and horni tend to be intermediate to those of anxius and g. liragus in both the structure and coloration of the anal forceps.

The characters Benoit (1965) used were worked out by Alexseev (1960). Among them was the location of a short macro-seta ("un pied petite") located in relation to a small circular depression or dimple in the cuticle. The dim-

¹Benoit (1965) does not specify the developmental stage of the larvae from which his measurements were taken.



Fig. 10. Labium of Agrilus granulatus liragus larva (X234). Note that the right palp is completely out of focus as with both in fig. 1B of Benoit (1965).

ples which are supposed to be associated with the pedalis structuralis (thoracic leg rudiments) are not evident on living larvae, and do not seem to be present with any regularity on specimens fixed in "XAAD" or by boiling. Consequently, the dimple may be the result of shrinking or swelling of the cuticle or associated tissues which may be related to the method of fixation and preservation. Benoit (1965) killed and preserved his larvae in 70 percent alcohol. There also seems to be the possibility that the absence of the depressions may have been related to the stage of larval development. Most of the larvae we examined had assumed the bent-over position in the pupal chamber. Benoit failed to mention the developmental state of the larvae he examined.

Benoit (1965) says there are also other marked differences between the larvae of anxius and g. liragus. As these require higher magnifications or more preparation, we did not examine Michigan material for these characters.

Pupae. There is nothing particularly unusual about the pupae of these species. All are creamy-white at first, and gradually assume the adult coloration. The eyes are the first parts to darken, and the elytra darken last. It appears to be during the period of pupal development that much of the adult structural variation arises, and it may very well be as much due to variation in the conditions under which the pupae develop as it is to genotypic variation.

GENERAL BIOLOGIES OF AGRILUS ANXIUS,

A. PENSUS, A. HORNI, AND

A. GRANULATUS LIRAGUS

Hosts and Ranges

THE BRONZE BIRCH BORER. A. anxius appears to be host specific to birches, Betula spp. Fisher (1928) lists the following birches as hosts for anxius: yellow birch, Betula lutea; paper birch, B. papyrifera; European white birch,

B. alba (and varieties); gray birch, B. populifolia; and sweet birch, B. lenta. Barter and Brown (1949) also list B. fontinalis as a host for anxius. Hitchcock, et al. (1964) rank this birch as a variety of the western paper birch, B. occidentalis, which is closely allied to B. papyrifera. Harlow and Harrar (1958), in fact, call the western paper birch B. papyrifera var. commutata.

Although it has been reared from numerous hosts, the principal hosts for anxius are the native paper birches, B. papyrifera and B. occidentalis. A. anxius is, then, primarily confined to northern forest types, but its range extends somewhat south of the range of B. papyrifera in the eastern U. S., where it is found even at low altitudes as far south as Washington, D. C. It ranges west to Oregon and British Columbia.

THE BRONZE POPLAR BORER. A. granulatus liragus has been reared from several Populus species, although its principal host is trembling aspen, Populus tremuloides. In addition, Barter (1965) lists the following as hosts for g. liragus: bigtooth aspen, P. grandidentata; eastern cottonwood, P. deltoides; balsam poplar, P. balsamifera ssp. balsamifera; and the black cottonwood, P. balsamifera ssp. trichocarpa (Torr. & Gray) Brayshaw (1965).

The known range of g. liragus is very similar to that of anxius, but g. liragus does not occur as far south as anxius does in the eastern U. S. The southern edge of the g. liragus range seems to comply more closely with the range of P. tremuloides than that of anxius does with the range of B. papyrifera. Just how far north either g. liragus or anxius occur is not known, but both have been taken as far north as Edmonton, Alberta. The former, at least, should occur in interior Alaska.

THE ASPEN ROOT GIRDLER. Trembling aspen is the principal horni host, but bigtooth aspen and balsam poplar are also infested. Infestation levels on balsam poplar are sometimes quite high.

When seed stock of various species of poplars are transplanted in experimental orchard-like plots, horni can be particularly troublesome. Nord et al. (1965) found that under these conditions, horni readily infests the Eurasian species Populus alba and P. tremula. He found that various hybrid aspens were also infested. In nature, however, horni is probably confined mostly to species which reproduce by root suckering (i. e. aspens and balsam poplars).

Although horni has not yet been found as far west as g. liragus, it is probably not because the former has a more limited distribution, but is more likely a reflection of the fact that horni is not collected as readily as is g. liragus. There are specimens in the U. S. National Museum from Massachusetts to Arizona, and as far north as Aweme, Manitoba.

THE ALDER-BIRCH BORER. A. pensus has been reared from Alnus rugosa and collected on the foliage of this shrub. It has also been found in abundance on the foliage of green alder, Alnus crispa according to Barter and Brown, (1949). Fisher (1928) described betulae, a synonym of pensus, from specimens reared from river birch (Betula nigra) and Knull (1930) reared a large series from that host. The records of Blanchard (1889) for Agrilus granulatus collected on alders refer to pensus¹, not to quadriguttatus as Fisher (1928) suggests. Records for pensus on Ostrya virginiana are of questionable significance. One specimen collected by C. A. Frost (Monmouth, Maine; June 23, 1910) is labeled "ironwood" and three by Geo. M. Greene (Philadelphia,

¹Horn (1891) described pensus from the series taken by Blanchard (1889).

Pennsylvania; May 24, 1900) are labeled "hophornbean."¹ Not only is it rather doubtful that pensus infests Ostrya, but it is entirely possible that alders or young birches were mistaken for Ostrya. Ironwood, at least, is an unlikely host because its ecology is so very different from that of alders and river birch. A. pensus has been collected as far west as Aweme, in southern Manitoba, and in the East occurs as far north as mid-New Brunswick (Barter and Brown, 1949). Manee (1913) recorded Agrilus granulatus on "black alder" at Southern Pines, North Carolina. As it was collected with Eupristocerus cogitans Weber (an agriline species that infests alders), the record should be considered to refer to Agrilus pensus.

Life Cycles

A. anxius and A. granulatus liragus have a two-year life cycle under some conditions, but a one-year life cycle when other conditions prevail. A. horni and A. pensus, however, seem to have obligatory two-year life cycles.

ANXIUS AND G. LIRAGUS. When the eggs of anxius and g. liragus are deposited on hosts that are dying, severely injured trees or blowdowns, for example, the larvae often construct the pupal chamber during the same season that the eggs were laid. On the other hand, when oviposition occurs on more vigorous hosts, a two year life cycle results (Balch and Prebble, 1940; Anderson, 1942; Barter, 1957, 1965). Nonetheless, the larvae of these species cannot survive in healthy trees, and successful larval development is always dependent upon the host being in a weakened condition because of drought, repeated unsuccessful borer attacks, or other injuries (Barter, 1957, 1965).

PENSUS. The habits of A. pensus have not been studied sufficiently to establish the usual condition of its host at the time of oviposition. We have never seen larval galleries that would indicate a life cycle of less than two years for pensus. Furthermore, the larvae appear to overwinter primarily in two stages. Mature larvae, of course, overwinter in the pupal chamber, and early instar larvae are found overwintering deep within the xylem. Blanchard (1889) says pensus "breeds in and frequents stems of partly dead alders, but does not appear on the foliage very much." Knull (1950) says it breeds in "unhealthy" river birches, but mentions nothing about the size of the trees infested. Fisher (1928) says the pupal cells are common in the stems of young river birches that have died, and we have similarly found that the adult emergence holes are common on dead alders. However, numerous speckled alders were examined for the presence of pensus larvae, and those which harbor immature larvae are invariably alive, and many of those infested with mature larvae or later stages have not succumbed completely. Because the larvae always seem to require more than one year to complete development, the adults probably never oviposit on hosts imminently near death.

Only one attempt was made to attract pensus with cut stems of alders. Although there was a pensus infestation in the area, none were attracted. Oviposition on such material would be detrimental for this species, because early death would be inevitable for the larvae. The bark of Alnus rugosa is so thin that the phloem would become moribund and dessicated much too quickly to

¹Specimens in U. S. National Museum, Washington, D. C.

permit larval development. However, it seems probable that even large, decisively injured or felled river birches are not attractive to pensus.

HORNI. Nord (1962) found no evidence of anything less than a two-year life cycle for horni, and those findings are supported by our observations. By examining suckers containing mature larvae it is often possible to establish when the first instar gallery was formed. First instar larvae feed in the phloem¹ while moving down the stem toward the root, but in no instance was a first instar gallery located in the phloem of suckers infested with mature larvae. When it was not obliterated by the larva when it re-entered the stem, the dark spot indicating the position of the first instar gallery was invariably found between the outer two rings of xylem.

Moreover, out of 60 larvae introduced into suckers of various sizes, 5 larvae completed their development during the second summer. One larva matured in the laboratory during the third summer, but no larvae matured during the first season.

Nord (1962) found that the total length of horni galleries varied between 40 and 90 inches. The maximum length of the galleries of anxius and g. liragus which mature in two years is about 52 inches. The galleries of anxius or g. liragus larvae completing their development in one year are usually less than half that long (cf Barter, 1957; Anderson, 1944). Thus the evidence is overwhelmingly against the occurrence of a one-year life cycle for horni. Two years are usually required for horni development to be completed, but occasionally it may take three years.

Developmental Patterns

HATCHING OF EGGS. Barter (1957, 1965) found that incubation of anxius and g. liragus eggs requires about two weeks. The same is true for horni, and is probably generally true of many Agrilus. When embryonic development is complete, the first larval instar bores out of the egg and into the bark of the host, leaving the egg shell packed with frass.

LARVAL FEEDING PERIOD. Although larval behavior differs among Agrilus species, certain generalities can be made. As with most Buprestidae, the larvae never bore exit holes for their frass, but instead pack it tightly into the gallery behind them.

Heering (1956) gives a very detailed account of the larval behavior of Agrilus viridis. Some aspects of its behavior seem very similar to those of anxius or g. liragus, and other aspects seem typical for Agrilus in general. The viridis larvae are pressed tightly into the gallery. According to Heering this allows the microscopic spinules on the lateral muscular ridges to grip the sides of the gallery. The larvae move forward by constricting and stretching the segments telescopically. Movement of the parts of the body besides the head and anal forceps is entirely restricted by the sides of the gallery.

All the tissues macerated by the larvae pass through the digestive tract. As the frass passes out the anus, it is clasped between the anal forceps. With these the larvae pack the frass tightly into the gallery behind them (Heering,

¹Nord et al. (1965) said that during the first stadium the larvae feed in the cortex, but this is the position of the gallery one year after it is formed.

1956). It would seem necessary that the frass be packed at least enough to make its density as great as that of the tissues on which the larvae feed.

The Bronze Birch and Bronze Poplar Borers. Barter (1957, 1965) says that after they bore out of the egg, the larvae move directly through the bark to the cambial¹ region, but Anderson (1944) found that some larvae bore as much as 10 inches in the bark while passing obliquely to the cambial region. These species mine chiefly in the phloem, but the xylem is also scored. Anderson (1944) found that after reaching the cambial region, the larvae feed for an average of 1.3, 3.9, 7.1, and 13.0 inches in each of the four larval stadia preceding the molt to the fifth instar, after which the pupal chamber is formed. This indicates that there is a correlation between larval size and the amount of feeding done in any stadium. In the trees from which Anderson accumulated these data the points at which molting occurred were marked by departures of the gallery into the xylem. In hosts of a very decadent nature the larvae usually do not bore into the xylem before molting. On the other hand, in the more vigorous hosts which can be successfully infested, there are likely to be more xylem departures than molts. Apparently, these xylem departures are elicited by the unfavorable conditions occurring when host vigor is comparatively high.

Host condition also has a bearing on other aspects of gallery formation. In severely weakened or very decadent hosts larval galleries usually show no distinct pattern. Under these conditions, the larvae follow a course suggesting that they feed on the freshest phloem they encounter (Barter, 1957). These galleries can be fairly straight, but they usually meander without any pattern in these kinds of hosts.

In more vigorous hosts a zig-zag or sinuate gallery pattern is the rule. Under these conditions anxius makes a gallery which progresses in the direction tended by the phloem sieve elements or the xylem vessels, but weaves back and forth across their grain forming a gallery with continually expanding hyperbolic links (figs. 11, 16). Under similar conditions the successive links

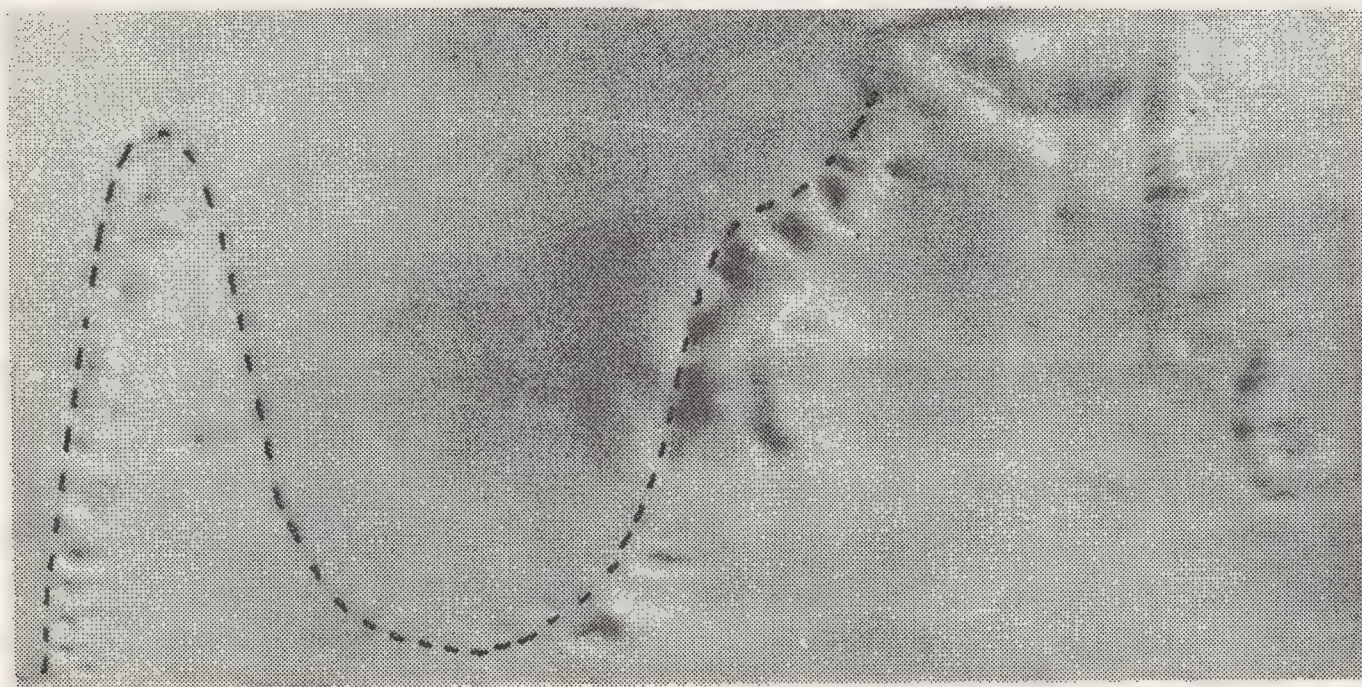


Fig. 11. Larval gallery of Agrilus anxius (in Betula papyrifera) that has healed over, indicating that it was made under conditions of high host resistance (from Anderson, 1944).

¹ Some authors suggest that these insects bore in the cambium. The cambium is extremely thin (strictly defined, a single cell thick; cf Esau, 1953) and, therefore, it is inaccurate to say that these insects bore in the cambium. Although the cambium may be consumed as an insignificant part of the nutriment, food value is more likely to be derived from its derivatives, particularly the phloem and perhaps the newly-formed xylem.

of the *g. liragus* gallery are much closer together, often lying adjacent to each other (fig. 12). The attempt to explain these gallery patterns will be deferred to the part of this section which deals with host resistance.

The Alder-Birch Borer. The larvae of *A. pensus* boring in the stems of *Alnus rugosa* often form galleries without any regular pattern. Sometimes, however, the gallery is sinuate like those of *anxius*, particularly those parts of the *pensus* gallery which do not lie deeply in the wood. Xylem departures are more frequent with *pensus* larvae, and sometimes they bore through the wood from one side of the stem to the other, a behavioral trait noted by Barter (1957) for *anxius* when it bores in branches.

According to Larsen (1901) *anxius* larvae make spiral galleries in branches. This has never been reported for *g. liragus*, and *pensus* does not form spiral galleries, even when it bores in alder branches only about an inch in diameter.

Only one case was encountered in which several *pensus* larvae had completely girdled the phloem¹, and this was only during the latter stages of larval development. Very little is known about the larval behavior of this species, but it seems clear that if the host dies during the earlier stages of larval development, they would be unable to complete their development (cf page 16). Perhaps for this reason, mass attack is not the habit of this insect.

The Aspen Root Girdler. Some aspects of *A. horni* development seem to differ radically from what is characteristic of *anxius*, *pensus*, and *g. liragus*. In *horni* and often in the others, eclosion from the egg is followed by direct entry into the phloem, but the first instar gallery is otherwise quite different in *horni*. The mechanism triggering the first molt of *horni* larvae appears to

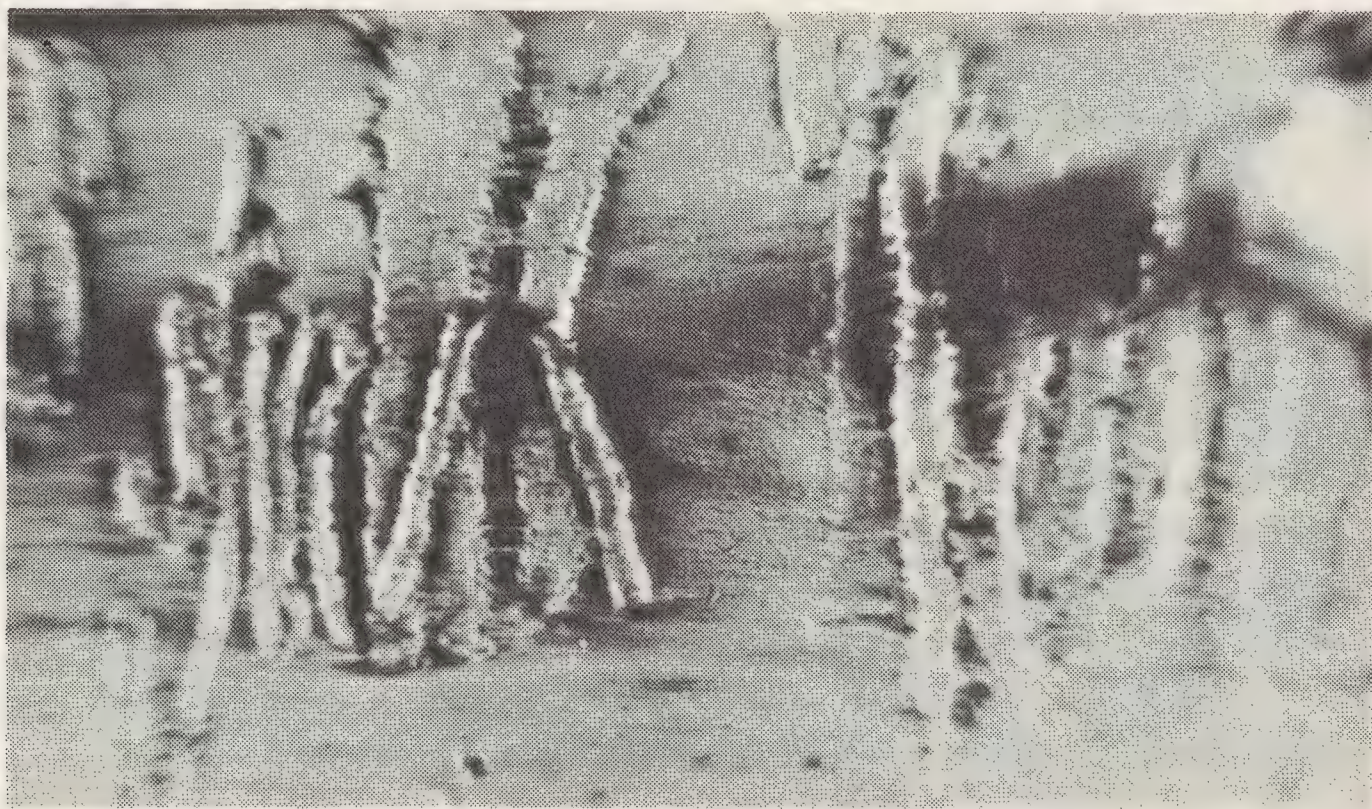


Fig. 12. Larval galleries of *Agrilus granulatus* (from area of intergradation of the nominate subspecies with *g. liragus* [see p. 85], but typical for the latter, at least). Some had healed over, indicating high host resistance (courtesy of R. E. Stevenson, Forest Biologist, Canada Dept. For. & Rural Dev., Calgary, Alberta).

¹Complete girdling may be more prevalent under some conditions than others. At Mallard Creek in Iron Co., Michigan, a moderately large *pensus* population build-up occurred one or two years after a stand of alders had been flooded by a beaver dam. In this area, alders that had been completely girdled by *pensus* were not rare (personal communication, 1968; R. P. Engel, University of Michigan, Ann Arbor).

be different, because the first instar galleries of this species are comparatively long. Prior to molting the first instar larvae of anxius and g. liragus bore an average of 1.3 inches after entering the phloem, although the gallery sometimes extends as much as 10 inches in the bark before it reaches the phloem (Anderson, 1944). In suckers recently killed by horni what appears to be the first instar gallery may extend out into a root for as much as 42 inches, and the total length of the first instar gallery usually is greater than 12 inches. Whether or not the first molt of the horni larvae occurs during the first season of development is unknown. No larvae have been found at this stage during the winter or spring. Presumably, they have been overlooked because of their small size (about 2 mm long in the first stadium).

Brooks (1914), presents an excellent discussion of the larval behavior of Agrilus vittaticollis Randall, which probably is a distant relative of horni (see fig. 44). He says that upon leaving the egg, the vittaticollis larva bores in the "cambium" (meaning cambial region) progressing down the trunk and into the root for a distance of 6 to 12 inches before boring into solid wood. For most of its length the gallery in the phloem is straight, generally following the grain of the wood. However, it sometimes zig-zags across the grain after leaving the egg, and invariably spirals once or twice in the phloem of the root before entering the xylem.

The larvae of horni behave similarly, but proceed with the grain until they enter the root. Just after reaching the root they are apt to make one or two spirals in the phloem, and often make others before they begin boring principally in the xylem. This behavior varies and may be dependent upon the size of the root and the condition of the host.

Sometimes the horni larvae do not bore in the xylem until they turn back toward the stem. In other instances they spiral in the xylem while still progressing away from the stem. Root diameter seems to be the factor determining where the larvae change the feeding direction. The turn is apparently elicited when the larvae reach a point where the diameter of the root they occupy is so small that they completely destroy the xylem. In aspens this is apt to occur where the root diameter is about $1/8$ to $3/16$ of an inch in diameter. The larvae may derive the stimulus eliciting the turn toward the stem when severing of the xylem results in different pressures on each side of the breach. While transpiration should make the pressure on the proximal side negative, any pressure in the distal part should be positive.

The turning point may be as much as 42 inches or more from the stem, but if the roots are short the larva may reverse its feeding direction only 6 inches from the stem. Instances in which the turning point is close to the stem are rare because the roots of aspen suckers are usually rather long.

The phloem in the roots of young aspen suckers is much thinner than that in aspen or birch stems suitable for infestation by g. liragus and anxius, respectively. The difference relates to the age-dependent accrument of inactive phloem. Although horni galleries lie principally within the xylem, it could hardly be otherwise. It appears that they consume the phloem too, and of all they ingest, the phloem probably provides most of what is assimilated.

After horni larvae re-enter the stem they sometimes bore a rather loosely spiralled or almost straight gallery which departs from the cambial region. Nord (1962), however, notes that the larvae always tunnel in the cambial region long enough to girdle the phloem. The root damage inflicted by horni larvae rarely seems to cause the death of suckers, because foliar discoloration occurs after the larvae return to the stem. Zahner and Debye (1962)

found that pruning only one half of the parent root of aspen suckers causes little mortality, even after two years. Consequently, horni-induced sucker mortality must be considered to result mostly from girdling of the stem.

The extent to which horni larvae feed in the cambial region after returning to the stem may be related to sucker vigor (Nord, 1962). Stager (1923) found that Agrilus aurichalceus Redtenbacher (= rubicola communis Obenberger) boring in bramble (Rubus spp.) stems increases or decreases the distance between spirals such that the stem does not die until the period of pupal maturity. Apparently, the death of the stem is a crucial factor, because Stäger says the pupae require a dry chamber. This seems to be true for species in the anxius group, as well. One might, therefore, expect variations in the position of horni pupal chambers to be at least partially related to moisture conditions in the stem at the time of its construction. Their pupal chambers are located an average of 4.8 inches above ground, but the position varies from a height of 2 inches to 14 inches. (Nord et al., 1965).

POST-FEEDING LARVAL PERIOD

Formation of the Pupal Chamber. Brooks (1914) made a detailed analysis of pupal chamber formation by A. vittaticollis. The vittaticollis larvae extend a burrow of the usual dimensions through to the bark at the upper end of the gallery. They then recede about 1/4 inch and begin eating wood from the sides of the gallery. As this proceeds, their feeding is directed backward along the ventral side of the body, thereby doubling the gallery diameter. The two ends of the body are, as a consequence, appressed closely together, and the head and anus soon lie side by side at the bottom of the pupal chamber. The chamber is then complete, but the larvae continue to move forward until the head and anus are at its upper end.

The larvae of all Agrilus spp. probably construct the pupal chamber similarly. However, when the layers of birch bark are gradually peeled off over anxius pupal chambers, a small loop in the gallery is found at the upper end of the chamber (exit point for imago). The loop apparently marks the point at which the larva turned in the bark and re-entered the xylem. It appears to be peculiar to anxius, and may somehow relate to the peculiarities of birch bark. The loop is not evident at the exit points constructed by g. liragus larvae, and horni and pensus, at least, must double back in the manner Brooks (1914) has observed for vittaticollis.

Shortening of the larva may be initiated earlier in most of the other species of the anxius group than it is in vittaticollis. Whereas vittaticollis initially settles in the pupal chamber with the body folded in half, the larvae of other species assume a position in which the body is folded between the second and third abdominal segments. While vittaticollis has both head and anus at the upper end of the chamber, the other species have the folded portion of the body at the upper end, the anus at the lower end, and the head pointed downward adjacent to the abdomen (in standing trees). This would indicate that instead of stopping where vittaticollis does, with head and anus at the upper end of the gallery, they move around farther. An alternative possibility is that after boring to the outer layers of bark, they merely turn back and feed along the ventral side of the body until the gallery width is doubled, then gradually recede or shrink to the overwintering position. This seems unlikely, however, as the exit point is plugged with frass. Unless these Agrilus have acquired the ability to pack frass with the mouth parts and head, it must be assumed that the anus, at some time, is at the upper end of the pupal chamber. Brooks

(1914) implies that it is the fourth instar vittaticollis larva which constructs the pupal chamber, which may explain the difference in the folding position for the abdomen in this species. The molt to the fifth instar occurs before formation of the pupal chamber in pensus, anxius, horni, and g. liragus, and the fifth instar larvae are noticeably shorter and more stout than fourth instar larvae.

Diapause. Barter (1947) has shown that it is necessary for anxius larvae to reach the fifth instar before overwintering in order for pupation to occur the following spring. He says that subjection of fifth instar larva in the pupal chamber to subfreezing temperatures is necessary for the continuation of development.

In early October 1966, some sections of a small birch tree infested with anxius were collected near Manistee, Michigan, and stored indoors with the intention of removing the larvae from them at leisure. In November part of them were debarked, and none of the larvae had shrunk to the prepupal form. In early December, however, adults emerged from these logs, and a few more issued in late December. Some larvae, on the other hand, did not enter the prepupal stage, suggesting that only some of them had been exposed to low temperatures in the proper stage and for a sufficient duration before they were brought indoors. This is in agreement with recent theories which, according to Wigglesworth (1964), suggest that diapause involves some phase of development that can proceed only at low temperatures.

While the transition from the overwintering stage to the prepupal stage may be possible only after some exposure to low temperatures, the transition itself appears to occur only when temperatures are above freezing, and probably considerably higher. In Michigan the transition of anxius, g. liragus, and horni larvae to the prepupal stage occurs during the spring. In Benzie Co., the transition of liragus larvae, in some cases, occurs before late April, but usually is later. In Iron Co. some horni larvae do not go into the prepupal stage until early June.

PUPAL TRANSITION. In Iron Co. the transition from the prepupa to the pupa usually occurs in May and early June for anxius, g. liragus, and horni. There is no delay in development when the pupal stage is reached, and soon after the all-white pupa forms it begins to take on some of the adult coloration. The eyes are the first parts to darken, and the mandibles darken next (Barter, 1957). The elytra remain white until most of the other parts of the body have darkened, and do not come to rest in the adult position until rather late in pupal development. Very likely, this is the reason that the wings are deformed more frequently than other parts in rearing these beetles. When drying of the wood around the pupal chamber is too rapid, the elytra may not take shape properly, after uncurling from the sides of the abdomen. This usually results in a poor fit of the elytra along the suture, causing a gap which exposes the membranous wings. Sometimes the deformities are more extreme.

ADULT EMERGENCE

Study Procedure. Eclosion of the adults from the pupal chamber was followed in several ways. Unfortunately, no good field emergence data were obtained for g. liragus, and no attempts were made to get records of field emergence for pensus.

In 1964 g. liragus emergence began about May 30, which was considerably earlier than was expected. Consequently, there was not sufficient time to locate enough pupal chambers for checking field emergence adequately. Some data were obtained by placing small triangular screen cages (fig. 13) over the

exit points that were exposed by cutting away the outer bark layers. The same method was employed in 1965, but because emergence was considerably delayed the results were extremely poor. Dessication of the exposed bark layers and wood prior to the beginning of the emergence period caused high mortality of the pupae and young adults.

The same type of cage worked well for analyzing field emergence of anxius. To expose the exit points for anxius adults, only a few outer layers of birch bark had to be removed. Consequently, the rate of dessication of inner bark and wood probably differed insignificantly from that of infested trees not treated in this way. A. anxius emerged normally from caged trees in 1964 and 1965. In 1964 the cages were checked intermittently, only often enough to roughly establish the beginning, end and peak period of emergence. In 1965 they were checked daily, except on days when emergence was unlikely.

In 1964 the emergence of horni adults was followed in the field by examining some infested suckers marked with flagging. Although the plot was checked only every other day, this method proved to be rather inefficient. Hence, different methods were used in 1965. The basal portions (sticks) of 123 infested P. tremuloides stems were placed in a clearing at the University of Michigan Forestry Camp near Beechwood, where they received full sunlight during the middle of the day. The ends of the sticks were waxed, and the pupal chambers were then located by comparing the sticks with their X-ray¹ negatives. Tubes of plastic screening were positioned over the segments of the sticks harboring the pupal chambers, and the ends of the tubes were constricted by stapling or taping. The sticks were held in an upright position near the ground by cords strung between stakes (fig. 14). They were checked daily.

It is probably safe to say that in most parts of their ranges, peak emergence for anxius, g. liragus, and horni occurs during June, but even within a given region there can be significant year-to-year variations in the emergence pattern. The variations in emergence periods relate to weather variations. Davis and Raghuvir (1964) compared deviations from long term mean air temperatures with emergence data for A. aurichalceus. The temperature data used were those for the month of March, April, and May. Walton (1951)

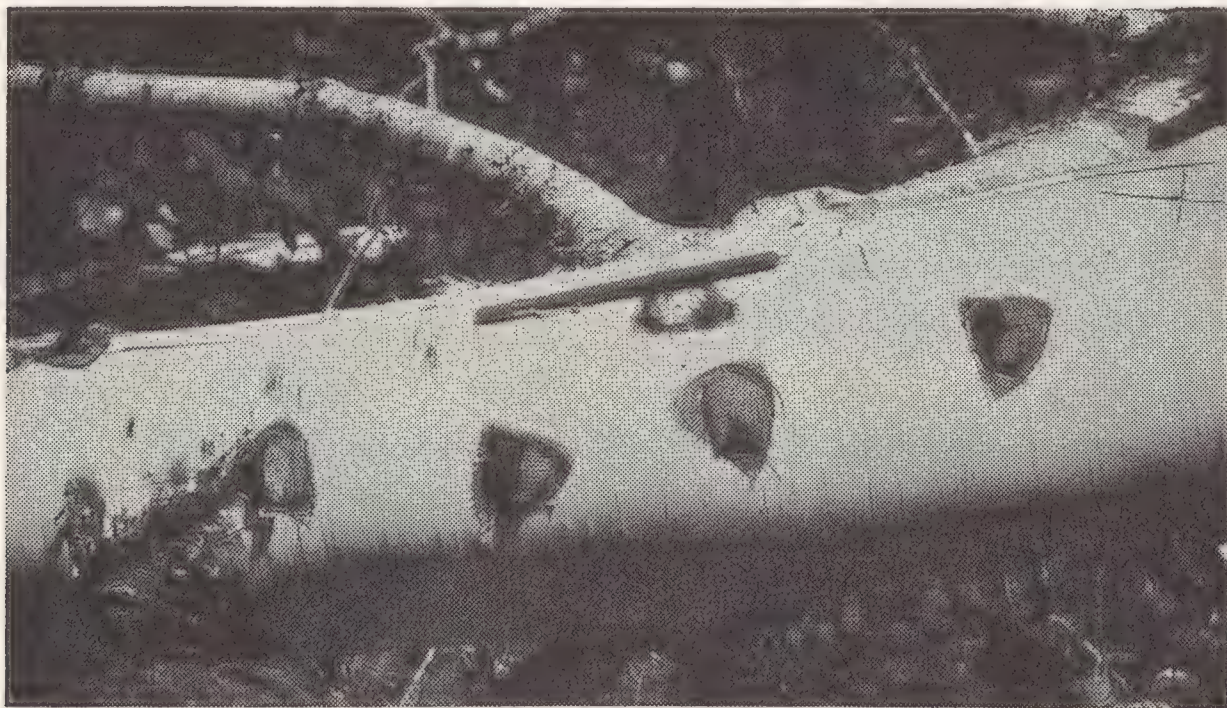


Fig. 13. Small emergence cages stapled over exit points for Agrilus anxius adults.

¹The X-ray machine and techniques used are discussed by Knight and Albertin (1966).



Fig. 14. Plot at Camp Filibert Roth near Beechwood, Michigan, where the emergence of Agrilus horni was studied under semi-natural conditions by stringing the infested sticks between stakes to hold them vertically.

employed the same technique for studying the emergence of A. ruficollis Fabricius for successive years. Emergence appears to be sufficiently well correlated with monthly temperature data to make the technique useful.

Results and Discussion. Table 1 shows the deviations from long term monthly means for Stambaugh, Michigan for March, April and May in 1964 and 1965 (U. S. Weather Bureau, 1964). The average deviation for 1964 was +0.97 degrees, while that for 1965 was -1.23 degrees. Emergence data for these two years reflect the differences.

In 1964 anxius emergence began in the Stambaugh vicinity about June 4 but not until June 14 in 1965. The difference between peak emergence times was even greater, being about June 7 or 9 in 1964, and between June 20 and 23 in 1965. In 1964 horni emergence began about June 7, but was delayed until about June 20 in 1965. Peak emergence was between June 9 and June 15 in 1964, while it occurred between June 21 and June 28 in 1965 (fig. 15).

The 1964 emergence periods of horni and anxius did not extend past the end of June, but in 1965 both species continued emerging into July. Surprisingly, one anxius adult was found alive in an emergence cage on August 4, but with this unusual exception, emergence of this species ended by July 7. A. horni emergence ended on July 15, making the duration of the 1965 emergence period about equal to that for 1964.

Table 1. Average deviation from long-term mean air temperature (F) for Stambaugh, Michigan.

Month	Year	
	1964	1965
March	-2.2	-5.6
April	+1.3	-2.1
May	+3.8	+4.0
Mean	+0.97	-1.23

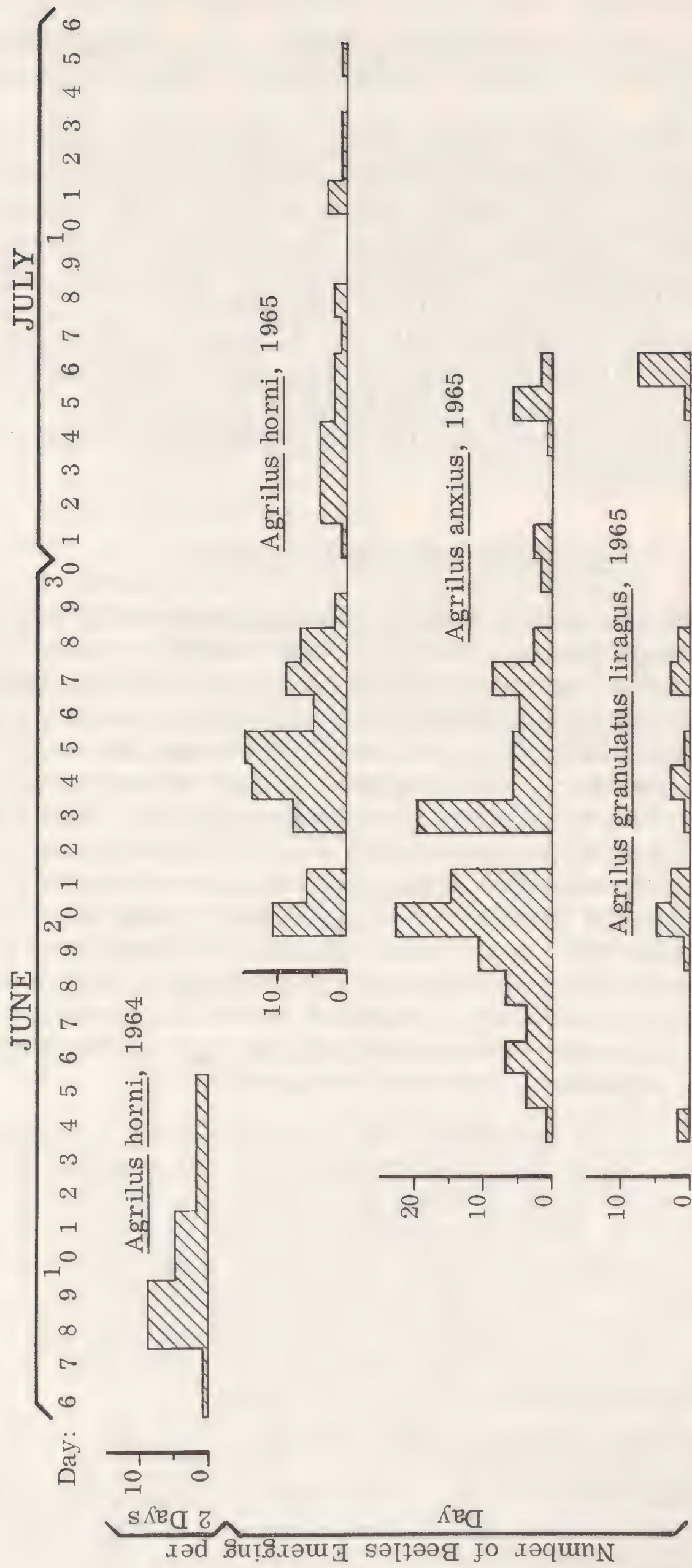


Fig. 15. Adult emergence dates of *Agrilus* spp. in Iron Co., Michigan. Note the following: (1) Five *horni* emergences occurred from the 16th through the 29th of June, 1964; for this interval the plot could not be checked and specific emergence dates are unknown. (2) One *anxius* adult was found alive in an emergence cage on August 4 and would have been dead if it had emerged more than 1 or 2 days before.

Barter (1949) found that the mean emergence dates for g. liragus preceded those for anxius by an average of 12.7 days. Although data obtained for g. liragus in our study were rather poor, it is evident that the differences in time of emergence are not as great in Michigan. A. g. liragus began emerging about 7 or 8 days before anxius in 1964, but the peak emergence periods were not as far apart.

Anderson (1944) reared both anxius and g. liragus from caged aspen and birch logs in Minnesota. He considered the possibility that he was working with two "host races," so one might assume that he would have noticed any significant difference in emergence times. In combining the emergence data for both anxius and g. liragus, Anderson found that emergence began on May 29 and ended on July 2, the peak occurring on June 10.

A difference in peak emergence times for g. liragus and anxius would appear to have no more real significance than any other differences between these species, and may be subject to the same kinds of geographic variation. These beetles are, in any case, actively mating and laying eggs during time spans which are nearly coextensive.

Population Regulating Factors

The factors which are usually considered important in the regulation of insect populations are parasites, predators, and weather conditions. There have been many semantic arguments devoted to the question of whether or not factors which cannot take an increasing toll on an organism as its density increases can be as important as factors that can increase their toll with density. Because factors like weather conditions have no way of responding to density, it is usually assumed that they fall in the former category. More often than not, though, weather conditions are clearly a part of the climatic scheme to which a species becomes adapted. There may be some variations of weather which occur so infrequently that they are not likely to bring about genetic adaptation in the species affected. Such catastrophic factors are here considered to be of secondary importance as population regulating factors; a species must, in the long run, be part of a density dependent controlling system. The factors likely to be of major importance in controlling the Agrilus being considered here, are parasites, predators, and host resistance.

HOST CONDITION. Host resistance can be regarded as an indirect effect of weather conditions, but it is probably more valid to consider it to be a manifestation of the more or less balanced relationship between the host and its phytophagous parasite, and a manifestation of the physiological condition of the host. The physiological condition of trees is most directly related to their age and site quality. By loosely applying these two variables one could explain most of the interactions which occur between Agrilus spp. and their hosts but the balance of the interrelationship is also influenced by parasites and predators, both phytophagous and entomophagous.

The Bronze Birch and Bronze Poplar Borers. Anderson (1944) says the larvae of anxius or g. liragus require living "cambium" if they are to complete their development successfully. Inner bark tissues which have died and turned brown are unsuitable for larval development. Barter (1957) found that some first instar anxius larvae may bore 13 to 18 inches without molting in moribund phloem. Those that are able to molt bore about twice as far (6 inches) as larvae feeding in phloem which has not turned brown. The evidence

seems to indicate that these larvae require nutrients associated with living phloem and that these essential nutrients decompose when the phloem cells die.

Swaine (1918) and Balch and Prebble (1940) reported finding anxius attacking and killing many healthy, mature birches in Canadian forests. Nash et al. (1951) reported that during times of high bronze birch borer population levels, healthy trees are attacked and killed. Different opinions were held by Spaulding and MacAloney (1931) and Hall (1933), who believed that the borer attacks birches because they are "dying." Barter (1957) suggests that the borer may appear to be more aggressive under outbreak conditions, but that it otherwise plays only a secondary role. He and Anderson (1944) present evidence showing that the beetles are usually unable to successfully attack healthy trees unless they are exposed to repeated unsuccessful borer attacks in successive years. Of course, after such repeated attacks, the trees could not be considered healthy, and persistent attacks of this sort could only occur during extended outbreaks. Perhaps unsuccessful attacks indicate that the number of susceptible trees is limited, or that "spill-over" occurs from highly attractive trees onto less attractive ones adjacent.

It is apparently only when many trees are simultaneously predisposed to infestation that the bronze birch borer becomes epidemic. A. granulatus liragus apparently does not often reach the outbreak state, but Barter (1965) and Barter and Cameron (1955) found that following repeated defoliation by the forest tent caterpillar, Malacosoma disstria Hber., aspens are predisposed to g. liragus infestation. Under such conditions g. liragus can cause deterioration and death of hosts it attacks either on branches or the main stem. Arru (1962) discusses the factors which predispose newly transplanted poplars in northern Italy to attacks of Agrilus suvorovi Obenberger (= viridis populnea Schaeffer). Problems with this insect arose only after poplars were planted on soils which were not as well suited to them as the deep friable soils to which poplar cultures were formerly confined. Arru believes that the factors which make the transplants susceptible to infestation by the beetle are those preventing resumption of growth following planting. The most important of them is moisture stress, which is likely to occur when poplars are transplanted on sandy or pebbly soils, on embankments, or in compact, poorly aerated soil.

Anderson (1944) treated aspens and birches in a number of ways to determine the severity of injury, if any, necessary to predispose them to the attacks of g. liragus and anxius¹. He made some interesting observations on brood development in 6 aspens and 6 birches which were girdled in September, 1940. All of these trees, except one of the aspens, remained alive throughout the summer of 1941, when they became infested with g. liragus and anxius. Brood density below the girdles in the aspens averaged 1.2 per sq ft (52 sq ft examined), while above the girdles there were only 0.1 larvae per sq ft (88 sq ft examined). Similar results were obtained for the birches. Below the girdles all the living borers were either pupae or adults, but only larvae were found above the girdles during the spring of 1942.

All of the trees produced a small annual ring above the girdle during the summer that they were attacked by Agrilus. No growth rings were produced below the girdles in any of these trees, however.

When Anderson (1944) debarked the girdled trees he found that the bark

¹Both taxa were still lumped under the name anxius at that time.

moisture content below the girdles was nearly 2 times that above. He assumed this to be a reflection of conditions that had existed during the previous summer. This assumption is incorrect because girdling trees by cutting through the phloem causes starvation and death of the roots. After the roots of a girdled tree die, water absorption ceases and the rest of the tree probably dies slowly from dessication (Kramer and Kozlowski, 1960). Because the phloem above the girdle continues to receive small amounts of carbohydrates, while that below gets none, the former should maintain a higher moisture content. It is the presence of solutes (sugars, etc.) in the phloem which allows its turgidity to be maintained. The diffusion pressure deficit of phloem sap offsets the effects of negative pressure or tension in the xylem. Therefore, the high bark moisture contents Anderson found below the girdles in the spring of 1942 were possible only because the bark had absorbed moisture during the winter. Hence, he has used a false premise in asserting that the larval mortality in trees with a proliferating cambium is not related to bark moisture content.

Heering (1956) found a relationship between bark moisture content and the susceptibility of beeches (*Fagus sylvatica*) to attack by *Agrilus viridis*. However, he claims that in some cases callose formation becomes the important host resistance factor, especially in trees so extensively dessicated that defensive sap flow is impossible. Because callose is a polysaccharide consisting of linked glucose units (Kessler, 1958), its formation involves a process much like normal growth. The growth of trees is probably controlled more by water availability than by any other environmental factor (Kozlowski, 1964), and deficits in water availability can cause physiological conditions which override growth regulatory processes (Zahner and Donnelly, 1967). It is, therefore, difficult to see how severely dessicated trees could form callose fast enough to pinch off continuously feeding larvae. The most logical explanation is that when Heering thought larval mortality was attributable to callose formation, the larvae had, in fact, been overwhelmed by phloem exudates, and were afterward being overgrown by callose. Even his own observations support this contention. He found that in very moist, vigorous bark, the *viridis* larvae construct vent holes ("Rindensaft-Abflusskanalen") which prevent sap from accumulating in the gallery by allowing it to drain off to the outside. The very fact that the larvae have time enough to cease forward movement and push the anterior part of the body through the bark, suggests that wound callose formation could not be rapid enough to kill them.

Heering (1956) found that the moisture content of bark infested with first instar larvae is almost as high as that of sound bark. This could indicate that bark which appears to be sound may really have low vigor, or instead, that his technique is too crude for measuring the essential differences between susceptible bark and bark resistant to infestation. He removed his bark samples from the trees, placed them in glasers' putty, and analyzed their moisture content in the laboratory. His index of tree resistance was bark moisture content expressed as a percentage of its total dry weight. This measure of host resistance is not precise because the active phloem constitutes a very small fraction of the total bark mass. Critical differences in its turgidity would be masked by variations in other bark factors, such as the amount of accumulated cork or inactive phloem. Perhaps a refinement of the technique, such as that used by Bier (1964) would give better results.

However, phloem pressure would probably be a better measure of active phloem borer resistance for the majority of woody angiosperms. Some of the angiosperms have gum ducts and may have resistance mechanisms analogous

to those of conifers. For some conifers a close relationship between oleoresin exudation pressure and tree resistance to scolytid attack has been demonstrated (see for example, Vit  , 1961). While the nature of conifer oleoresin ducts and their products makes pressure measurements relatively easy, host resistance could not be studied as readily for species whose chief resistance mechanism is the exudation of phloem sap. Piercing the phloem causes an injury which interferes with its normal activity. However, the observations of Heering (1956) suggest that useful pressure measurements might be obtained without tapping the active phloem itself. He says that even before the heads of newly-hatched Agrilus viridis larvae have completely entered the bark, they are often repelled by exuding sap which detaches the egg shell from the bark. Without the shell to push against the larvae are helpless.

If, as it appears, phloem pressure is actually the most important host resistance factor encountered by phloem feeding Agrilus it should follow that the serpentine galleries, like those often produced by g. liragus and anxius are an adaptation giving them some advantage for withstanding the copious flow of sap. In starting a zig-zag or sinuate gallery pattern, a larva makes an initial cross-grain segment, then turns abruptly and reverses its direction. When it begins to bore past the lateral extent of the gallery segment to which it is adjacent, the larva usually reverses its direction.

Heering (1956) believed that the sinuate galleries produced by Agrilus viridis larvae are the consequence of a fixed pattern of behavior, although they do not follow a sinuate course in very decadent hosts. Barter (1965), on the other hand, found that g. liragus makes galleries with very close transverse segments in relatively vigorous hosts, while in more decadent ones the gallery becomes more sinuous resembling those of anxius. Like xylem departures, which for anxius or g. liragus increase in number with increasing host vigor, the zig-zag or sinuate gallery pattern may be elicited as a sort of avoidance reaction.

There seems to be little reason for assuming that the effect of phloem sap on the larvae could be anything other than simple suffocation. Presumably, when the larvae make departures into the xylem, the plug of frass behind them protects them from the copious influx of phloem sap. The advantages which might be derived from a serpentine gallery pattern are more nebulous, however.

Barter (1957) suggested that by staying beneath the previously formed parts of the gallery, the larvae are protected from the downward, translocation of sap. However, downward progressing galleries do not seem to prevail over those progressing upward in standing trees. Barter (1957) knew that galleries can proceed in either direction, and his hypothesis is, therefore, inadequate, even for explaining the facts as he knew them.

Moreover, there seems to be good reason for believing that movement of sap in the phloem of even the most vigorous of trees which Agrilus can infest is, at most, very slight. Trees susceptible to Agrilus infestation are not healthy and, without exception, must be subject to high internal moisture stress. According to the mass-flow theory, phloem transport occurs from areas of higher osmotic sap concentration to regions of lower concentration. During the growing season, the direction of transport would normally be from the crown toward the roots. However, when trees are under severe moisture stress, the rate of respiration in the crown may equal or exceed that of gross photosynthesis. Under such conditions there may be no transport of carbohydrates in the phloem, and its turgidity must become significantly lower than

in trees not under moisture stress.

Furthermore, serpentine or zig-zag galleries are produced even in logs, if they are infested rather soon after being cut. This is strong evidence suggesting that they are produced in response to local turgidity rather than to the mass flow accompanying the translocation of carbohydrates. It seems fairly apparent that even when moisture stress is too great for the translocation of carbohydrates to occur, the phloem is still sufficiently turgid for sap to infuse into sieve elements that have been severed. When *Agrilus* larvae cut through the sieve tubes, part of the exuding sap is probably absorbed by the inactive phloem and the xylem. Consequently, the pressure of sap in gallery should be lower than that in the surrounding phloem. In spite of the fact that successful infestation must invariably be attended by low turgidity in the phloem, sap should pass slowly from it until it loses its turgidity entirely or until its pressure comes into equilibrium with that in the gallery.

If the foregoing premises are valid, the function of the sinuate or zig-zag gallery pattern may be unrelated to phloem transport or to minimizing the amount of sap that enters the gallery. It seems possible that they minimize only the detrimental effects of sap oozing from newly-severed sieve elements, as is illustrated in figure 16. When a larva turns back adjacent to the prior-formed gallery link, the phloem inside the turn is cut off between the links forming a peninsula. These peninsulas should not exude as much sap as the phloem outside the turn. The minimization of sap influx from the peninsula might make it possible for the larvae to minimize its suffocating effects by opening the spiracles on the side of the body adjacent to the peninsula. With each successive link, then, the larvae could open the spiracles on alternate

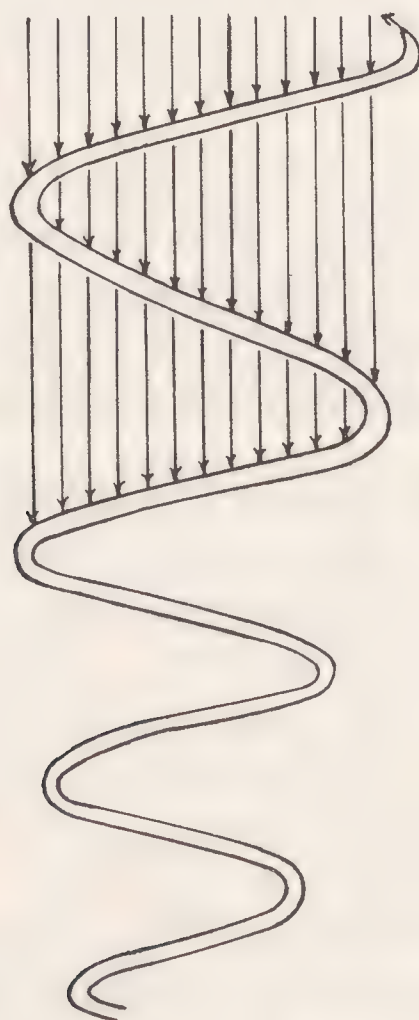


Fig. 16. Sinuate gallery pattern similar to that of *Agrilus anxius*. The vertical arrows indicate the hypothesized direction of sap infusion into the gallery after severing of the phloem sieve elements (no active transport is occurring). Because the body of the larva is a-pressed very tightly to the walls of the gallery, alternately opening the spiracles on the side of the body exposed to the smallest amount of sap infusion, might allow continual respiration.

sides of the body.

The differences in the pattern of the g. liragus and anxius galleries may be partially related to differences in the phloem structure of birches and poplars. It is not sound evolutionary thinking to assert that the gallery differences are attributable either to genetic differences in the insect species or purely to differences in the hosts. In other words, it is pointless to try to separate the combined phenotypic effects of environment and genotype.

A. anxius or g. liragus larvae in relatively vigorous hosts construct longer galleries than those living in weaker hosts. Barter (1957) found that anxius which matured in one season in rapidly dying birches, made galleries of only 15 to 20 inches, while those in more vigorous trees matured in two years, after boring 20 to 52 inches. Anderson (1944) gives similar data for g. liragus development. The reason for the vigor-related variations in gallery length are apparently unknown, but two possibilities are evident: (1) larvae feeding in relatively vigorous tissues perhaps must expend more energy in attaining the nutrients necessary for complete development, or (2) molting of late larval stadia may occur only under certain conditions, such as those relating to host physiology, time of year, or both. There are no published data from which it is possible to ascertain if the gallery segments for all larval stadia are longer in more vigorous hosts or if the increase in gallery length is built up during a particular portion of larval development.

The Alder-Birch Borer. Very little is known about the relationship between Agrilus pensus and its hosts, Alnus spp. and Betula nigra. Because it is often difficult to distinguish pensus-infested speckled alders (Alnus rugosa) from uninfested ones, it seems likely that pensus plays a more primary role in causing the death of these shrubs than do g. liragus and anxius in infesting their respective hosts.

It is very difficult to trace out complete pensus galleries because they meander extensively through the xylem and a number of galleries may intersect. Consequently, no attempts were made to accumulate data on total gallery length. It seems likely, though, that the average length of pensus galleries will approach the maximum length for anxius or g. liragus galleries. Because dying speckled alders are probably not suitable hosts for pensus, these insects are always contending with a level of host resistance which is found only in the more vigorous of the hosts suitable for anxius or g. liragus. Moreover, many speckled alders show signs of unsuccessful attacks, and successful ones do not seem to occur very frequently. Much of the earlier portion of larval life is spent in the xylem, and the mortality rate of young larvae seems to be very high.

Blanchard (1889) records one location in Massachusetts where he found pensus (under the name granulatus) in rather large numbers. Barter and Brown (1949) collected a large series of pensus on Alnus crispa var. mollis and suggest that it is particularly well-adapted to this alder, which is confined to the Atlantic seaboard. However, A. c. var. mollis does not appear to differ greatly in form or in habitat from A. rugosa. Furthermore, in June, 1968 an area in which pensus adults were moderately abundant was encountered at Mallard Creek in Iron Co., Michigan. The creek bottom was flooded by beavers during the previous summer and possibly also in the summer of 1966. It, therefore, appears that, at least throughout most of its range, pensus becomes numerous only infrequently, particularly because of the host resistance controlling factor.

The Aspen Root Girdler. Agrilus horni has different means for coping

with host resistance than have anxius, liragus, or pensus. First of all, rather than attacking dead or dying hosts, it limits its attacks to those poplar suckers small enough to be overwhelmed, and those on which eggs are deposited appear to be of normal vigor. The vigor of aspen suckers must be affected by the root girdling of horni larvae. Zahner and Debyle (1965) found that pruning either of the parental roots of Populus grandidentata suckers about 4 or 5 years old usually causes a significant reduction in the growth of the suckers over a span of two growing seasons following treatment. Usually, horni larvae completely masticate the xylem in one of the roots in which they bore. This occurs at a point where the diameter of the root is about 1/8 to 3/16 of an inch in diameter, and its chief function may be to elicit the turn of the larva back toward the stem of the host (see page 20). However, because water absorption occurs mainly in a zone 1 to 10 cm from the apex of a root (Kozlowski, 1964), the xylem girdling may induce moisture stress or increase it in the stem of the host and in the part of the root proximal to the girdle. If the xylem girdle occurs in a branch of a main (or parental) root, or if it sometimes does not occur at all, the survival of larvae may depend upon their ability to effectively girdle the phloem, thereby causing starvation in the distal part of the root or preventing food from reaching the stem and proximal part of the root from the parent tree (ortet). There are probably definite size limits on roots which can be effectively girdled in either manner.

In 1960 Nord (1962) measured the diameters of 150 horni-killed suckers. He found that 84 percent of these had diameters of 0.5 inches or less. He was, however, unable to demonstrate that horni shows a preference for small suckers because a similar percentage of the suckers in the stand he sampled had diameters below 0.5 inches. Studying the same area in 1962, Fowler (1963) found that 71 percent of the infested suckers had diameters below 0.5 inches, while about 76 percent of the healthy ones were below that size. Using regression and variance analysis, he compared the relationship of sucker height to diameter for infested suckers with that for uninfested ones, and found no difference. His illustrations show the two sets of height-diameter data to be strikingly congruent.

Fowler (1963) lists the numbers of infested and uninfested suckers in each of the age classes from 1 to 6 years, and his data are presented in table 2.

Table 2. Age-class frequency distribution of healthy and Agrilus-killed Populus tremuloides suckers.^a

Age	Number of Suckers	
	Healthy	<u>horni</u> -Killed
1	0	1
2	3	13
3	19	58
4	55	51
5	53	23
6	20	4
Total	150	150

^aModified from Fowler (1963).

When the two distributions are made comparable by subtracting one year from the age of the healthy suckers, it can be seen that the age-class frequencies of infested and uninfested ones are very similar. It must be remembered that suckers which died at age X were actually selected by females at age X-1. Hence, the suckers available to horni females in this area were from 1 to 4 years old. The maximum height of suckers in the area would have been about 6.5 feet. This is near the maximum size of suckers on which horni eggs have been found.

The data of Nord (1962) and Fowler (1963) seem to indicate that the horni females were ovipositing randomly with respect to sucker size. It appears that when the eggs were laid, few of the suckers were too large to elicit oviposition, or that too few were sufficiently above the optimum size for survival of larvae to make it apparent in the statistics.

A small experiment was initiated in 1964 to examine the effects of host resistance on horni larvae. Four groups of 15 Populus tremuloides suckers were chosen with the intention of introducing first instar horni larvae at their bases. Two groups were composed of suckers beginning their second year of growth, and the other two groups of suckers were starting their fourth growing season. They will be referred to as 2-year-old and 4-year-old suckers.

An area was picked in which the likelihood of having the experiment confounded by natural infestation was low, although this approach, admittedly, has undesirabilities. A random sample of the heights of 2 and 4-year old suckers was taken. Heights were measured with a leveling rod and were recorded to within the nearest one-tenth foot of the point where the previous season's growth terminated.

The mean heights were calculated for each age class. Within each age group, height classes of ± 1 standard deviation from the mean were set as the sizes for suckers to be chosen for the experiment. The resultant height values for 2-year suckers were 1.3 and 3.2 feet, while those for 4-year-old suckers were 3.7 and 7.4 feet. These treatments will be referred to as 2-year-, 2-year+, 4-year-, and 4-year+, respectively. On selecting the suckers for the experiment a ± 0.2 foot leeway from the treatment value was allowed.

Eggs for rearing the horni larvae were procured from 10 cheesecloth cages which were placed over individual aspen suckers (fig. 17 and 18). A pair of beetles was introduced into each of the cages, and the eggs were collected periodically. The eggs were removed in groups by cutting away a portion of the bark on which they had been deposited. After the eggs were removed additional soil was placed in the can which enclosed the base of the suckers so that subsequent oviposition would occur on smooth, uninjured bark.

The eggs and bark to which they adhered were placed in small incubators, which consisted of 1 by 3 inch white pine blocks with five shallow depressions made with a 1/4 inch drill (fig. 19). The eggs were placed in the depressions and a microscope slide was fastened over the tops of the blocks with masking tape. To keep the incubators moist, dampened paper toweling stapled to wood strips was held in contact with the ends of the wood blocks by rubber bands. The pan in which the incubators were placed was covered to prevent dessication.

A camel hair brush was used for transferring larvae. They were placed in small petri dishes lined with moistened blotting paper and transferred to the test suckers as soon as possible. The larvae were placed in small cavities cut in the bark about one inch above the sucker bases. The cavities were



Fig. 17. Unassembled cheesecloth cage for Agrilus horni oviposition.



Fig. 18. Assembled cheesecloth cage for Agrilus horni oviposition.

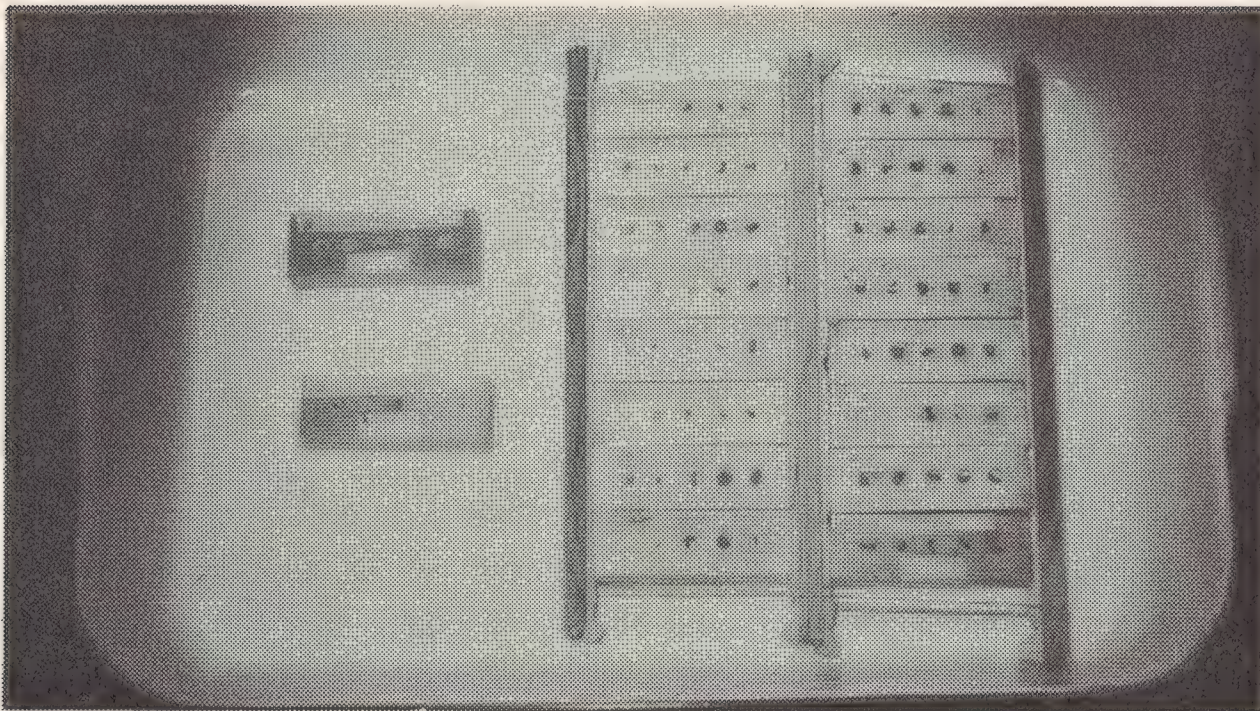


Fig. 19. Wooden incubators for *Agrilus* eggs. Standard microscope slides (1 X 3 inches) are taped over the tops to cover the small depressions holding the eggs.

prepared with a sharp scalpel by making two horizontal incisions about one eighth inch apart through the bark to the surface of the xylem. The incisions were cut obliquely downward so that when the strip of bark between them was pried out, the cavity formed would keep the wriggling larvae from falling out.

After the larvae were placed in the cavities, they were covered over with tape. Test suckers were subsequently revisited for checking on the survival of the larvae. Those which had died before boring into the exposed phloem region were replaced. All dead larvae were replaced until all suckers harbored larvae which had started into the phloem. It was necessary to replace seventeen larvae before all suckers were infested, although it was apparent when the suckers were examined in 1966 that some of the larvae probably died after boring a very short distance. Introductions were begun on July 25 and completed on July 31, 1964. A few days following completion of the introductions, the cavities in the bark were filled with grafting compound to prevent fungal infection or dessication at these points.

Evaluations were made by digging up the suckers and their roots on May 4 and 5, 1966. The larval galleries were traced by cutting into the stems and roots with a sharp knife. The results are tabulated in table 3. It can be seen that only one larva matured in a 2 year- sucker, and none completed development in the 4 year+ suckers. Six of the larvae which eventually formed pupal chambers were in the 2 year+ (2) and 4 year- (4) suckers.

The data are, of course, rather meager, but it is likely that survival in the 2 year- and 4 year+ treatment was poor primarily because of the unfavorable conditions for the larvae in the roots. In 6 of the 2 year- suckers the larvae had to bore in roots that were, perhaps, too small to allow successful development. Larvae are known to have successfully matured after spiraling over a span of only about 6 inches in small roots, but this is probably not always possible. Survival of *horni* larvae was probably impossible in three of the suckers having roots of adequate size, because the roots were diseased and decomposing at various points.

One of the 2 year- suckers had a very large root, about 1 1/2 inches in diameter. Such large roots probably are not suitable for *horni* larvae either,

Table 3. Development of Agrilus horni larvae in selected Populus tremuloides root suckers.

Treatment ^a	Number of Larvae		
	Boring at Least Short Gallery	Boring More Than 10 Inches	Completing Development
2yr-	14	8	1
2yr+	14	8	2
4yr-	11	5	4
4yr+	11	4	0
All	50	25	7

^aSuckers were in their second (2yr) and fourth (4yr) growing seasons when larvae were introduced and had heights (± 0.2 ft; see p. 33) of 1.3 ft (2yr-), 3.2 ft (2yr+), 3.7 ft (4yr-), and 7.4 ft (4yr+).

probably because they cannot be girdled readily. Large root size was undoubtedly an important factor contributing to mortality in 4 year+ suckers too, but some of the larvae in these suckers seem to have perished even before reaching the roots.

All the information so far assembled indicates that horni can kill healthy aspen suckers. However, there is an upper limit to the size of hosts it can subdue. It also seems likely that, if other factors are equivalent, the suckers on areas of good site quality are able to resist infestation better than those on poor sites. The areas in which horni is likely to establish persistent populations are ones where suckers spring up in fields at the edges of stands of larger aspens or in areas where the aspen clones do not expand rapidly to fill the intervening spaces. The site quality in such locations is usually low even in the former case, but is invariably poor in the latter. A. horni is usually not found in areas of high site quality, and never becomes abundant on such sites. Nevertheless, one should not assume that their scarcity in areas of high site quality is directly related to the poor survival of larvae in these areas. The horni adults seem to orient to open areas, and good sites usually produce dense, closed stands. Moreover, the adults may have evolved this affinity for open areas at least partly through the effects of genetic selection channelled via differential survival of the larvae.

Poor aspen sites which are left rather denuded after fire, like the main study area of Nord (1962) and Fowler (1963) are likely to be good horni habitats after the aspens have suckered. The numbers of horni in such places should decrease rapidly over a period of 6 to 8 years, however. In fact, in 1964, approximately four years following the year of peak abundance, there were only a few horni-infested suckers to be found on the plot where Nord and Fowler had worked. The largest infested suckers listed in their data had diameters of 1.0 inches (6 inches above base). A. horni eggs were not found on suckers larger than 0.9 inches at the base. It appears as though host selection may be the factor limiting the sizes of suckers which are actually infested. Again, the crucial survival factor would appear to be root size, and this certainly correlates rather well with stem size. Although host resistance may not directly limit the upper size of suckers in which horni larvae can live (i.e., by simply causing the mortality of those above the upper limit) one must presume that adult host selection behavior is evolutionarily directed by the ultimate results

of it.

PREDATORS. Woodpeckers are the only predators known to exert any population limiting effect on anxius and g. liragus. Their predation on g. liragus is confined to standing trees (Barter, 1965), and the same is probably true for woodpecker predation on anxius. Knight (1958) found that the feeding of woodpeckers on bark beetles has the greatest effect when the beetle infestations are heavy and infested trees are concentrated. Similarly, Barter (1957) found that their predation on anxius appears to be more prevalent in heavily infested trees. One might then expect that the effectiveness of this predation would be rather variable depending upon the size and concentration of populations, although other factors are probably also important. Nash et al. (1951) found that the toll of woodpeckers on anxius varied from very slight in some areas to as high as 30 percent in others. Barter (1957, 1965), however, found that woodpeckers consumed as much as 50 percent of anxius brood, and removed up to 40 percent of the g. liragus brood from their pupal cells. Anderson (1944) says that about 10 percent of anxius and g. liragus prepupae were consumed by woodpeckers.

Woodpecker predation is confined to the spring, apparently occurring only after the larvae begin the transition to the prepupal stage. Barter (1957) believed that woodpeckers fed on anxius at that time only, but later (1965) he found that the pupae of g. liragus were consumed and presumed that adults were also eaten.

Woodpeckers are also an important population limiting factor for pensus. It appears that the predation on pensus occurs during the winter. Large numbers of pensus brood are never found in a single Alnus rugosa stem, but the extent of concentration of infested alders may affect woodpecker activity. It seems that once a woodpecker finds the first pensus pupal chamber in a stem he is likely to find them all, although there usually are not more than 7 or 8 in a single stem.

We have seen spiders and ants attacking the adults of g. liragus and anxius, but they probably cause little mortality. These beetles usually apress the legs to the thorax and fall free of the host in time to avoid being caught. In one instance, however, an ant had grasped its falling prey and both predator and prey fell to the ground where they couldn't be found. The quickness with which these beetles take flight or drop to the ground, especially on hot days, is apparently reflected in Gory's name anxius (nomen nudum of Dejean), and it seems rather unique that torpidus Leconte has been placed as a synonym of the former.

Nord et al. (1965) observed ants mouthing the eggs of horni on caged aspen suckers. Since ants frequently pass up and down the stems of suckers, often in visits to sources of aphid honey dew, they may encounter the horni eggs which are placed above ground level. Because many eggs survive to hatch, they do not appear to be particularly attractive to ants, however.

PARASITES. Nash et al. (1951) listed eight parasite species which were reared in cages containing logs infested with anxius. It is certain that some of the Ichneumonidae they list as anxius parasites were instead reared from other insects¹. Glypta sp. and Pimpla sp. are parasites of Lepidoptera, while

¹Identifications made for Nash et al. were undoubtedly reliable as they say these were made by Townes and Muesebeck, both prominent specialists.

Olesicampe sp. is a sawfly parasite. None of these could have been reared from anxius.

The parasite Barter (1957) reared from birches was identified for him as Ephialtes sp., but has more recently been identified as Dolichomitus messor perlongus Cresson¹. The Ephialtes species reared from Populus by Barter (1965) is probably the same species. The parasite identified for Nash et al. (1951) as Ichneumon sp. is probably Dolichomitus sp., perhaps D. messor perlongus. Nomenclatural corrections in the usage of Ephialtes Schrank and Ichneumon L. have reinstated their application to groups parasitic on Lepidoptera².

Townes and Townes (1960) record D. messor perlongus as being reared from Saperda calcarata Say, and S. concolor Leconte, and it also parasitizes Oberea shaumii Leconte. Townes³ expresses doubt that females of messor perlongus could develop on Agrilus spp.

The records of several braconids reared by Nash et al. (1951) from anxius are probably legitimate. The species are Atanycolus charus Riley, Spathius simillimus Ashmead, and Doryctes atripes Provancher. They also reared the chalcid, Phasgonophora sulcata Westwood.

Barter (1957) reared an additional braconid from anxius, Helconidea ligator Say, but did not rear Doryctes. However, he records Doryctes sp. parasitizing g. liragus (Barter, 1965). Besides the Ephialtes sp. already discussed, other parasites Barter reared from g. liragus were Atanycolus charus, Phasgonophora sulcata, and the eulophid, Tetrastichus sp., listed as probably being near rugglesi Rowher.

Barter (1957) says that Atanycolus and Phasgonophora were the most important larval parasites of anxius, parasitizing 1 to 52 percent (average 14 percent) and 1 to 8 percent (average 4 percent) of the larvae, respectively. Other parasites were recovered only occasionally. He recovered parasites from only 9 percent of all larvae in his samples. Therefore it appears that total parasitism was not usually as great as is indicated by the percentages listed above, which were calculated for a sample of 600 larvae.

The only parasites which was consistently reared from g. liragus larvae by Barter (1965) is Phasgonophora sulcata, which parasitized from 2 to 20 percent of the larvae. Other parasites were reared less frequently.

Parasitism on larvae of anxius and g. liragus may amount to a rather insignificant portion of the total mortality factors which regulate their populations. The same cannot be said for egg parasitism, however. Barter (1957, 1965) and Nash et al. (1951) found that parasitism was consistently high on eggs of anxius and g. liragus, usually being near 50 percent for both species. Apparently, two chalcidoids were about equally important, even though in in-

¹The specimens reared from Betula were lent to us by Mr. Barter for identification, but those he reared from Populus has been accidentally destroyed.

²The revision of the Ephialtinae by Townes and Townes (1960) had led to the change for Ephialtes, and Ichneumon, sensu Townes (1944), included Dolichomitus, sensu Townes (1960).

³Personal communication, 1966; H. K. Townes, American Entomological Institute, Ann Arbor, Michigan.

dividual cases the species were alternately dominant. One was identified as Thysanus sp. (Thysanidae) and the other is an encyrtid near Coccidencyrtus.

While the egg parasites of anxius and g. liragus must be more important in population regulation than the parasites of the larvae and pupae, the reverse seems to hold for horni. Only four eggs in a sample of 147 (about 3 percent) taken in 1965 were found to be parasitized. The parasite was identified as Oobius sp.¹

Although they are exposed to parasites for a shorter time than the larvae of g. liragus or anxius, horni larvae are parasitized much more heavily. A. horni pupae are also parasitized rather frequently. Total parasitism of larvae and pupae was about 42 percent in 847 rearings, with Tetrastichus nordi Burks being reared most often. This eulophid is quite small and probably lays its eggs on the larvae when they spiral just beneath the bark in the stem, between the time of their emergence from the root and formation of the pupal chamber. This was deduced from observing the behavior of a few T. nordi females in the laboratory and from X-ray pictures of T. nordi larvae developing just beneath the bark on larvae that never formed a pupal chamber. Usually, however, the horni larvae are not killed by Tetrastichus until after the pupal chamber is formed.

Emergence of T. nordi adults corresponds with the time when horni larvae are re-entering the sucker stems (August and early September). An average of 49.1 ± 17.1 adults emerged in a sample of 49 broods. The size of the adults and their sex ratio is quite variable.

Three ichneumonids were found with about equal frequency in horni pupal chambers. They parasitized a combined average of approximately 13 percent of the horni collected. These parasites have longer ovipositors, enabling them to place eggs on the larvae and pupae within their pupal chambers. Xylophrurus agrili Viereck has been reared from horni larvae and pupae in both spring and fall. Brooks (1914) says this species has two generations per year. He found it to be an important parasite of A. vittaticollis, which bores in the roots of various trees and shrubs of the family Roseaceae. In the fall it lays its eggs on the vittaticollis larvae at about the time they are forming the pupal chamber. The spring brood attacks pupae or larvae just prior to pupation. A. vittaticollis may be the primary host for X. agrili, as Brooks found it to destroy from 25 to 40 percent of the larvae and pupae of this beetle.

Xylophrurus bicolor maurus Townes emerged from horni pupal cells only during the spring, and all of the collecting and rearing records which Townes and Townes (1962) list for X. bicolor indicate that the adults fly only during the spring. X. bicolor seems to have a diapause similar to that of many Agrilus spp., requiring an extended period of cold for development to be completed. It is perhaps for this reason that efforts to rear the adults from suckers collected during the initial stages of larval development are not very successful.

No rearing records were previously available for X. bicolor maurus. However, the western subspecies, X. bicolor bicolor has been reared from an insect in Salix sp. and from Saperda moesta Leconte infesting Populus balsamifera ssp. trichocarpa (Townes and Townes, 1960).

The third ichneumonid, Mastrus smithii Packard, was incapable of emerging from horni pupal cells. The only adults obtained were removed from the infested suckers where they died, often after boring only part of an exit hole.

¹Determined by B. D. Burks, U. S. Dept. Agr., A.R.S., Entomology Res. Div., Washington, D. C.

The mandibular teeth of these specimens are usually worn considerably. This species is known to be a secondary parasite on the ichneumon fly Gambrus extrematus Cresson and has been reared from the cocoons of two sawfly species (Townes, 1951). It seems likely that it is poorly adapted for emerging from Agrilus pupal cells, and probably parasitizes ichneumonid parasites of other insects with greater success, particularly those in the cocoons of cecropia moths.

Besides Tetrastichus nordi, several other Chalcidoidea¹ were reared from horni pupal chambers. They caused about 6 percent mortality of the horni reared in this study, and this was attributed principally to Lampoterma sp.², a pteromalid. This parasite emerges about mid-May, and therefore, oviposits chiefly on prepupae or pupae of horni. From 3 to 10 adults develop in each horni pupal chamber. This Lampoterma sp. appears to be limited to one generation per year by an obligatory pupal diapause.

Eurytoma magdalis Ashmead (Eurytomidae) was reared from several horni pupal cells, but this species may be a secondary parasite. In two instances it is known to have emerged from pupal chambers which harbored two different types of parasite larvae.

Some of the larvae and pupae which died for unknown reasons (17.7 percent) may have been killed by parasite stings. Consequently, the impact of parasitism may be underestimated.

ADULT BEHAVIOR

Feeding and Maturation

Barter (1957) found that Agrilus anxius females, maintained in the laboratory, fed about 6 days before showing any tendency to lay eggs. Adults of anxius and g. liragus are not found mating or ovipositing in the field until about 2 weeks following emergence. There is no reason to suspect that the same is not true for horni and pensus.

Ogushi (1963) found that under laboratory conditions Agrilus auriventris auriventris Saunders females formed ova 5 to 6 days after emergence, but full grown ova were not present until 8 to 10 days after emergence. Oviposition began on or after the eleventh day following adult eclosion. Ogushi found no full-grown ovaries in females which had not fed. Their development was very slow in unfed beetles, many of which did not live long enough to reach the oviposition stage.

Similar developmental requirements are probably common to most, if not all, Agrilus. Some unfed anxius females dissected quite soon after emergence had partially developed ova. Without food, however, these females are probably unable to form fully-developed eggs, and usually die after a rather short time.

A. anxius adults were maintained successfully during the winter on pieces

¹Determined by B. D. Burks, U. S. Dept. Agr., A.R.S., Entomology Res. Div., Washington, D. C.

²Nord et al. (1965) list this species as Metastenus sp., but the application of Metastenus has recently been changed (cf Burks, 1967).

of apple, but in nature their feeding is, no doubt, restricted to leaves. Hutchings (1923a) says the bronze birch borer feeds more readily on the foliage of poplars and willows than on birch. Barter (1957) found that anxius adults consume the leaves of poplars, particularly those of Populus tremuloides, more readily than those of Betula papyrifera. The findings of Nash et al. (1951) differ slightly; in their laboratory studies anxius showed the greatest preference for P. grandidentata foliage. They rate the species used in their tests in the following order of decreasing preference: P. grandidentata, P. tremuloides, Salix spp., Betula lutea (= alleghaniensis), B. papyrifera, P. balsamifera, and Alnus spp.

Very little is known about the feeding habits of anxius adults, but they were occasionally observed feeding on B. papyrifera leaves by Barter (1957). Britton (1922) says bronze birch borer adults (those attacking birches) fly about and feed to some extent on the foliage of willow, poplar, and probably birch.

We have not tried feeding horni adults anything besides P. tremuloides leaves in the laboratory, and horni was found in the field on no plant other than tremuloides. Aspen leaves undoubtedly comprise the major portion of the adult horni diet, which is probably true for g. liragus also.

A. pensus, on the other hand, did not readily consume the foliage of aspens. Because they have been collected on the foliage of alders, but not on other plants, one would expect them to show some specificity for alder leaves. However, the only foliage which they seemed to eat readily in the laboratory was that of Salix spp. Very little testing with alder was possible, however, as the beetles were maintained in Ann Arbor, where alders are not readily available. Usually, pensus adults did not survive for more than a few days, no matter what kind of foliage they were provided. Adults of other species kept in the same controlled environment chambers survived exceptionally well (at 70 percent relative humidity; day temp 75°, night temp 60° F). The poor survival of pensus adults may have resulted because of a failure to provide the proper temperature and humidity for pupal development.

Dispersal

Nothing has been written about the dispersal capacities of g. liragus or anxius, and little is known about the dispersal of any Agrilus, including the ones that are naturalized pests in the United States. Heering (1956) has apparently made the only attempts at release and recapture studies with marked Agrilus. However, as only 200 A. viridis adults were released he was unable to recapture enough to give a reliable result.

Although Agrilus beetles may be capable of flying considerable distances, they probably do so only rarely. In rearing and maintaining these beetles in the laboratory we have seen nothing which would indicate the existence of any sort of antagonistic mechanism by which "flight exercise" acts as a releaser for feeding or reproductive activity as has been demonstrated for some aphids (Kennedy and Booth, 1963) and scolytid beetles (Graham, 1959, 1961). If they flew only far enough to encounter suitable hosts, they would usually be staying quite near the places where they emerged.

Host Selection

Following the period of reproductive maturation the adults are attracted

to the hosts which have the particular attributes making them suitable for mating and oviposition. Many Agrilus and other Buprestidae seem to show a strong tendency to select hosts which are well exposed to sunlight. Consequently, those which live on trees are most active at forest edges or in park-like stands.

ANXIUS AND G. LIRAGUS. Generally, anxius females are said to oviposit on the sunny sides of trees and on those most exposed to sunlight. However, Barter (1957) found that the photopositive tendencies of anxius can be overridden, to some extent, by other stimuli, presumably olfactory ones. Barter says that when the shady sides of trees are wounded, females oviposit there rather than on the unshaded side. He concluded that the olfactory response is often stronger than the photopositive response.

Anderson (1944) came to similar conclusions. During the first season of his two-year study he found no deviation from the commonly accepted idea that trees exposed to full sunlight attract significantly greater numbers of anxius and g. liragus than shaded ones. Using a 30 second counting interval Anderson found an average of 2.6 beetles per unshaded tree, while only 1.8 were found on shaded trees. When the experiment was repeated the following year, however, he found that the count for unshaded trees did not differ significantly from that for shaded trees. During the first season, trees with the tops broken off by winter damage were abundant, but such damage did not occur during the second year. Anderson thinks that greater numbers of weakened hosts were available during the first season, allowing g. liragus to make a selection for those more exposed to sunlight. His conclusion is that the physiological condition of the host is more important than its degree of exposure to sunlight.

There may be sexual differences in the photopositive response, but little has been done so far to account for the possibility. Males and virgin females may be more photopositive than ovipositing females. Females ovipositing on fallen trees are apt to work along the sides of stems on days when males orient more towards the upper surface.

One is prone to confuse the effects of light and temperature. It seems quite likely that these beetles will appear to be more photopositive on relatively cool days (but still above 70° F) than on hot days. An observation made in 1964, during studies of anxius behavior, illustrates this point. In order to concentrate the beetles on bolts cut from freshly-felled birches, the tops and other unused parts of the birches were pulled well into the shade. This slash, nevertheless, attracted some of the beetles, and the bolts under observation, which were in full sunlight, attracted only moderate numbers of them. That day the temperature maximum was 85° F (U. S. Weather Bureau, 1964; Stambaugh, 15 July) and the sky was clear, so that temperatures may actually have been too high for the insects to remain for extended periods in the direct sunlight.

In another of Anderson's (1944) experiments, the attractiveness of 7 types of host material was evaluated by tallying the numbers of adult g. liragus on each aspen test tree during a 30 second counting interval. Observations were made between 10 AM and 3 PM on sunny days when the shade temperature was between 75° and 90° F. His results are presented in table 4, and it is quite evident that injured trees are more likely to be attacked than uninjured ones. Barter (1957) found this to be true for anxius also. From Anderson's data (table 4) one may also surmise that standing trees are more attractive to g. liragus than similarly treated trees which are felled. Both the topped trees and topped and girdled trees attracted significantly greater numbers of beetles than trees which were felled. Perhaps this occurred because the standing trees

Table 4. Attractiveness of various types of Populus tremuloides host material to Agrilus granulatus liragus.^a

Condition of Host Trees	Average Number of Beetles per Tree per Observation ^{b,c}	Number of Observations
1. Vigorous	0	67
2. Suppressed	0	21
3. Girdled	0.1	54
4. Topped	1.9	54
5. Topped and girdled	2.8	27
6. Felled and lopped	1.0	27
7. Felled, not lopped	1.3	27

^aModified from Anderson (1944).

^bThe values are corrected so that each represents the number of beetles observed per 17 ft² of bark area, the average for all test trees.

^cThe only statistically significant differences are those between numbers not included within the span of a single vertical line.

were more fully exposed to sunlight than felled ones. In any case, these results could be misleading because standing trees rarely are as decisively injured by natural factors as are trees which are artificially topped or topped and girdled. The only natural injury which is really comparable occurs when trees are blown over. Less decisive natural injuries occur to standing trees when the tops are broken by winter ice damage or when the tops of already decrepit trees break where the wood exposed by repeated insect attack and disease becomes dry and brittle. Aspens are frequently victims of this type of injury, since the wood of these species is not particularly tough, and because they are often severely attacked by wood borers like Saperda calcarata and fungal parasites like Hypoxyylon pruinatum for a period of years before they finally succumb.

One might also conclude from the data of table 4 that both suppressed and vigorous trees are unattractive to g. liragus. In testing this more thoroughly, Anderson used an extended observation period of 14 days, to detect occasional beetles that might be attracted to the trees. This was facilitated by placing sheets of fly paper on the trunks of 10 paired aspens, each pair composed of a vigorous and a suppressed tree. During the 14 day observation period 18 beetles were caught by the fly paper on suppressed trees, but none were caught on vigorous trees. It is apparent that g. liragus is able to detect trees which are in poor condition, whether or not they have been wounded. The stimulus is undoubtedly olfactory, and is presumed to arise from the decomposition of substances in the bark or phloem. The attractiveness of the host may, in turn, depend upon the rate of decomposition, which is no doubt enhanced by injury.

HORNI. Theoretically, the kind of host selection exhibited by anxius and g. liragus should allow adult feeding to be separated from the activities involved in host selection. If this is true, then there might not be any highly developed specificity shown by feeding adults. In the late 1800's, buprestid collectors clearly recognized that the identity of an Agrilus larval host was not necessarily

indicated by the kind of foliage the adults are taken on. Perhaps this point is over-emphasized, because the adults of some kinds of species, like horni, may show more specificity in feeding, because feeding may be involved in the host selection process. Agrilus horni does not fly directly to the stems of aspen suckers, but instead lands on the foliage. The adults of this species usually feed before moving onto the stem where mating and oviposition occur. Whether or not they always feed before crawling from the foliage to the stem is not known. Nord et al. (1965) found that after caged horni females oviposit they move up to the foliage of suckers, resting and feeding for about 10 minutes before descending to lay another egg. Under natural conditions the females may usually ascend the stem following oviposition and fly to another sucker before feeding.

A. horni can maneuver with agility in flight, and can hover before landing. Their flight behavior indicates that they probably recognize aspen foliage before landing on it. If so, olfaction is clearly part of the recognition process. If the odors which direct them to the host do not, at least in part, emanate from the foliage, one would expect them to land frequently on the foliage of plants other than Populus spp. This was observed only once, when a male which had just mated flew from P. tremuloides sucker to a fern next to it, staying briefly before he flew back to the same aspen sucker and began feeding.

To go no farther than suggesting that horni recognizes its host by some characteristics of the foliage would be forming a hypothesis of very little value. Obviously, other factors must strongly influence the host selection of these beetles, as they do not live on just any species of Populus, or just any P. tremuloides sucker.

Previous Studies. Fowler (1963) studied the relationship of height, age, and stand density of aspen suckers to infestation by horni. He counted the number of infested and uninfested suckers on systematically located millacre quadrats. A graph of Fowler's data (fig. 20) appears to indicate that the unit-area density of horni-infested suckers is rather directly related to the unit-area density of all suckers.¹ However, it is not necessarily true that unit-area densities per se of the aspen suckers were the important variables affecting the infestation levels throughout Fowler's study area. It seems likely that some of the lower stand density values can be attributed to parts of it where the initial establishment of suckers was poor because of severe competition with other plants which dominated. Besides patches of sweet fern (Myrica asplenifolia [= Comptonia peregrina]), leather leaf (Chamaedaphne calyculata), and blueberry (Vaccinium spp.), there were young red pines (Pinus resinosa) scattered about. Quadrats with high sucker counts, on the other hand, may simply have occurred in places where some of the suckers were not shaded by other plants. In fact, high-count quadrats probably fell where suckers were clumped (fig. 21), and sucker clumps probably had originated in spots that were left denuded after the 1957 fire. Fowler (1963) notes that when infested suckers were associated with clumps, they were usually at the outer edges of them. A majority of the infested suckers in this may have occurred at the outer edges of clumps. Therefore, the contagion evident in the distribution of infested suckers may have resulted from strong contagion in the distribution of suckers suitable for oviposition.

¹A much more detailed analysis of the data is presented by Carlson (1968).

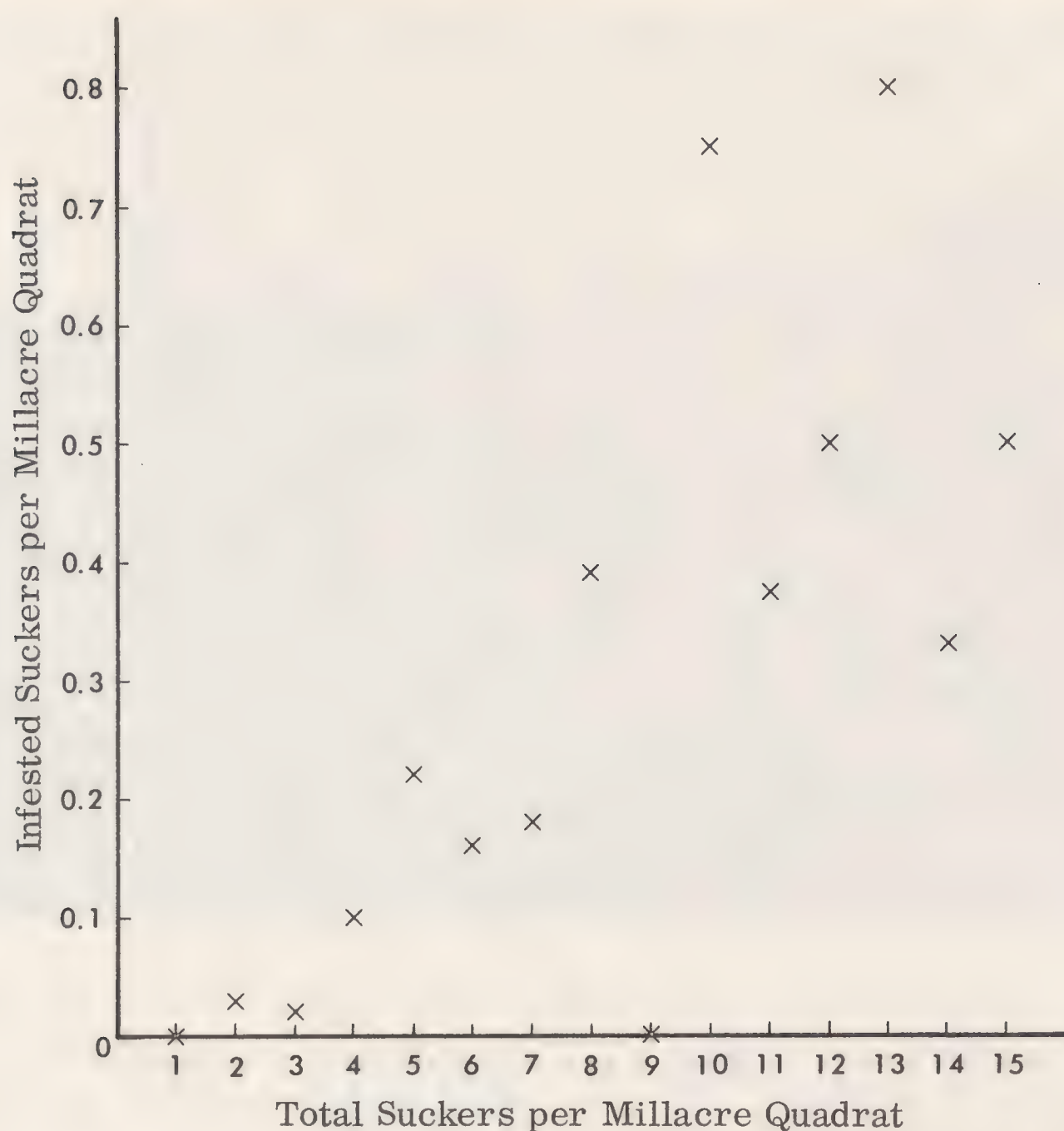


Fig. 20. Unit area density of horni-infested Populus tremuloides suckers as a function of stand density of all tremuloides suckers in the area sampled by Fowler (1963).

New Studies

Methods. The possibility that some contagion in egg distribution could occur independently of the distribution of suitable hosts has not been overlooked. In the spring of 1964 an area with an evenaged stand of aspen suckers was selected for studying this problem. It is an area near Beechwood, Michigan, where furrowing for the planting of pines had caused prolific root suckering by scattered, mature Populus tremuloides, some of which were still standing, while others had been pushed over (fig. 22).

Because the problem involved determining the spatial distribution of infested or egg-bearing suckers in relation to each other, there was little need for using standard sampling methods for estimating density (i.e. stems/unit area). Instead, it was decided that the problem could be best approached by using distance measurements as indicators of spatial relationships. The two variables measured were: (1) the distance from predetermined sampling points to the nearest infested or egg-bearing sucker (DNS) and (2) distance between each infested or egg-bearing sucker and the nearest neighboring infested or egg-bearing one (DNN). Sampling points were located systematically. Five plot centers were established, four at the corners of a 400 foot square and one in its center and also approximately centered within the study area.

Around each of the plot centers, 8 sampling points were established on a circle with a 50 foot radius. Sampling point number 1 was always located due north of the plot center, and the others were located at subsequent azimuthal intervals of 45 degrees. Sample distances were measured with a 100 foot tape.



Fig. 21. A spot in the study area of Nord (1962) and Fowler (1963), showing the clumped distribution of Populus tremuloides suckers and abundance of competing vegetation (from Nord, 1962). The aspen suckers occurred under similar conditions throughout much of the area.



Fig. 22. Agrilus horni study area near Beechwood, Michigan. The stand of Populus tremuloides suckers, which is relatively uniform in distribution, developed following furrowing for the planting of pines. Equipment used in the furrowing operation pushed over many of the mature aspens.

The Wilcoxon matched-pairs signed-ranks test (Siegel, 1956) was used for analyzing the data. Discussion of the results is deferred until later, where the results of a number of analyses are discussed together.

While evenaged sucker stands are best for studying the distribution of eggs by females, independent of sucker distribution, they are not well suited to studying the sucker size selection of horni females. For this, unevenaged areas are more appropriate. Unevenaged sucker areas occur in the ecotones between aspen forests and open fields or in park-like stands where clones or multiclone groups are apt to stand isolated, annually producing some suckers at their edges. Such areas are also of particular interest because they harbor more perpetual infestations than do evenaged stands. Devising sampling techniques for unevenaged areas was problematical, however. The most perplexing difficulty is that in these areas the zone in which the horni infestation occurs represents a rather small proportion of the ecotone area. Hence, it is difficult, if not impossible, to devise a random sampling scheme that is efficient. Even a systematic approach is difficult to contrive because the habitat of interest is usually distributed in a rather irregular manner. Therefore, the usual kinds of systematic procedures are not applicable.

The compromise devised cannot be considered ideally objective, but that does not seem to greatly impair its value. The sampling was carried out by proceeding along the edges of the clumps or closed stands of larger aspens and selecting the first 6 ft sucker encountered as a plot center. In turn, the 7 ft, 5 ft, 4 ft, 3 ft, 2 ft, and 1 ft suckers nearest the 6 ft one were selected¹.

The distance between the 6 ft sucker and each of the others (D_6) was measured. Before the suckers were chopped free at their roots and examined for eggs, the distance to the nearest neighboring sucker in the same height category (DNN) was measured and recorded. Only the first set of suckers selected was examined for horni eggs. Besides tallying the numbers of eggs and noting their positions, we also recorded the basal diameters of the suckers (DAB).

Successive plots were always separated by at least 3 times the maximum D_6 . Six foot suckers were chosen for the sampling centers because they were near the upper size limit for suckers which would bear horni eggs. Consequently, choosing a 6 ft sucker would insure that sampling would include areas where suckers above the upper size limit occurred, while still keeping it within areas that were likely to be horni habitat.

This sampling method was employed in one area near Kenton, Michigan and in another near Phelps, Wisconsin. Analyses of the data chiefly involved the use of chi-square comparisons and graphic procedures. Expected values (E_x) for the chi-square analyses were derived from expectancy factors (E_f), which are weighting factors based upon D_6 and DNN (collectively, D values) measurements. The basis for the computation of expected values is the assumption that the abundance of suckers in a particular size class is inversely related to the area of a circle which has a radius equal to the average D value for the class. Hence, density is proportional to $1/D^2$. In deriving the E_f values it was anticipated that DNN measurements should account for any clumping tendency among suckers of the same age. On the other hand, the D_6 measurements should account for any stratification that existed, such as gradients in the positions of suckers relative to those of other sizes. E_f values are computed simply by dividing the $1/D^2$ value for each size class by the total for all

¹Each height class had a ± 0.5 ft interval.

classes (giving each E_i relativity to all others). The expected numbers of egg-bearing suckers are derived by multiplying the total observed number of egg-bearing suckers by each E_i value.

One set of chi-square comparisons was made for height classes, and in another set the numbers of egg-bearing suckers were apportioned into DAB classes (table 6). Diameter class (DAB) values for the latter comparisons were computed from regressions of DAB over sucker height by substituting the values for the height class limits into the equation and solving for DAB.

To compare height and DAB as indicators of the suitability of suckers for horni oviposition, ratios of observed to expected values are used. This required the computation of additional expected values for a set of DAB classes with uniform limits. It was necessary to derive expected values for these uniform DAB classes indirectly, because there was no direct (significant) statistical relationship between DAB and D values.

In order that all ratios of observed to expected values have positive signs, it is necessary to adjust all expected values (E_x) upward so that none is exceeded by the observed (O_x) value for the same class. What was done, in effect, was to multiply all E_x values by the greatest O_x/E_x ratio occurring among all sucker classes (yielding E_{xo}). The subsequently derived O_x/E_{xo} ratios can be used for making between-area data comparisons as well as for the height-DAB comparison mentioned above. Factors with similar uses are derived by dividing the total number of eggs (S) occurring on the suckers of each size class by the corresponding E_{xo} values.

Discussion. There were no significant differences between DNS (distance to nearest sucker) and DNN (distance to nearest neighbor) measurements for either the infested or the egg-bearing suckers at the Beechwood, Michigan evenaged sucker stand. Therefore, there is no marked tendency toward contagion in the distribution of either infested or egg-bearing suckers. Two obvious explanations are possible. (1) A. horni females may make a post-oviposition flight, before they re-align and lay another egg. This sort of behavior should lead to a rather random distribution of eggs. (2) On the other hand, suckers which were suitable for oviposition and subsequent infestation may have been rather randomly distributed throughout the area.

The latter explanation seems to be the most logical. The few direct field observations made on horni females would indicate that they really do not fly very far before landing on another sucker. Nor is there any indication that a post-oviposition flight is an unvarying occurrence in a fixed behavioral pattern. Nord et al. (1965) found that after ovipositing, caged horni females immediately crawled up the sucker stem and out onto a leaf. After spending about 10 minutes feeding and "resting," they might descend to lay another egg, and so on.

Under natural conditions horni females may usually fly to another sucker after each egg is laid. It may be uncommon for them to feed on a sucker just after ovipositing on it, particularly if feeding is an integral part of the host selection process. In the Beechwood area only a few suckers were found with two horni eggs, and only one had three. When more than one egg had been placed on a given sucker, there was usually no way of knowing from their appearance if they had been deposited at about the same time or at different times. Unlike the Beechwood area, the egg-bearing suckers in the Phelps and Kenton areas usually had more than one egg (average 2.5) and one had a surprising total of 15 (table 5). When the difference between the latter areas and the Beechwood area are considered, it is only reasonable to conclude that the oc-

Table 5. The occurrence of *Agrilus horni* eggs in the Kenton and Phelps areas on *Populus tremuloides* root suckers in height classes of 1 to 7 ft.

Sucker Height Class (feet)	Suckers Sampled	Suckers bearing no eggs	Suckers Bearing Eggs							Number of Eggs	
			Categorized by Number of Eggs per Sucker							Total	Average per Egg-Bearing Sucker
			1	2	3	4	5	9	15		
1	30	29	1							1	1.0
2	30	23	3	3	1					7	1.7
3	30	21	3	1		3		1	1	9	4.5
4	30	16	6	4	2		2			14	2.1
5	30	20	3	3	3			1		10	2.7
6	30	22	5		3					8	1.7
7	30	26	2	1		1				4	2.0
All	210	157	23	12	9	4	2	2	1	53	2.5

currence of more than one egg on a single sucker is usually not an indication that they were laid in sequence by the same female. Instead, what seems to be indicated is that some suckers were far more suitable for *horni* oviposition than others, even of the same size. Moreover, in the Phelps and Kenton areas the *horni* habitat was restricted to a very narrow zone, and movement along it probably resulted in these beetles contacting suckers in particular locations more frequently than others. The most reasonable conclusion seems to be that when suckers in these particular locations were otherwise favorable for oviposition there were a number of eggs laid on them.

Sucker size should be an important factor affecting the distribution of eggs by *horni* females and/or the survival of the larvae. In both height and DAB chi-square comparisons the difference between the observed and expected distribution of eggs is highly significant (table 6). The relationship of egg occurrence to DAB is more sensitive than that with sucker height (figs. 23-26).

The Kenton trend line of O_x/E_{x_a} over DAB (fig. 24) shows a double peak, but the second peak is reduced in the graph of S/E_{x_a} over DAB (fig. 26). This suggests that in the Phelps area the suckers most likely to elicit *horni* oviposition had somewhat larger diameters than those in the Kenton area. This appears to be true despite the fact that the abundance of small suckers relative to those of larger sizes was greater in the Phelps area. Examination of the data on egg placement for the two areas yields the most likely reason for this difference. In the Phelps area more eggs were located in association with moss than on other kinds of deposition sites. Most of those Phelps area eggs deposited in association with moss occurred on the 0.6 and 0.7 inch suckers (all but 2 out of 21), and these two DAB classes were the source of the greatest difference between the areas. Therefore, it seems very likely that the occurrence of mosses on these suckers in the Phelps area is responsible for the positive skewing of the trend lines (figs. 24, 26) as compared to the more negatively skewed ones for the Kenton area.

Inasmuch as factors independent of sucker size, such as the occurrence of mosses, affect *horni* oviposition, even two areas with nearly identical arrays of sucker sizes will not necessarily have similar frequency distributions for those bearing eggs. In general, however, the data do strongly indicate this much: suckers between 0.3 and 0.9 inches DAB are most likely to elicit oviposition.

Table 6. Chi-square comparison of observed and expected size-class frequency distributions of Populus tremuloides suckers bearing Agrilus horni eggs in the Kenton and Phelps areas.

Area	Height Class (feet)	Egg-Bearing Suckers			χ^2	DAB Class (inches)	Egg-Bearing Suckers			χ^2
		Observed (O _x)	Expected (E _t X Σ O _x)				Observed (O _x)	Expected (E _t X Σ O _x)		
Kenton	1	1	8.13	6.25	< 0.211	2	8.13	4.62		
	2	4	6.83	1.17	0.222 - 0.358	3	6.83	2.15		
	3	5	5.16	0.00	0.359 - 0.505	10	5.16	4.54		
	4	9	3.57	8.26	0.506 - 0.652	5	3.57	0.57		
	5	4	2.26	1.34	0.653 - 0.808	6	2.26	6.19		
	6	3	1.32	2.14	0.809 - 0.955	2	1.32	0.23		
	7	2	0.73	2.21	> 0.955	0	0.73	0.73		
Total		28	28.00	21.37**		28	28.00	19.03**		
Phelps	1	0	11.50	11.50	< 0.179	0	11.50	11.50		
	2	2	6.31	2.94	0.180 - 0.287	2	6.30	2.93		
	3	3	3.59	0.10	0.288 - 0.395	3	3.59	0.10		
	4	6	2.10	7.24	0.396 - 0.503	8	2.10	16.58		
	5	7	1.26	26.15	0.504 - 0.611	4	1.26	2.40		
	6	6	0.77	35.52	0.612 - 0.719	4	0.77	13.55		
	7	2	0.47	4.98	> 0.719	3	0.47	13.62		
Total		26	26.00	88.43**		24†	24.00	60.68**		

† Total differs from that for height comparison because two DAB values are missing.

** Statistically significant at the 0.01 probability level.

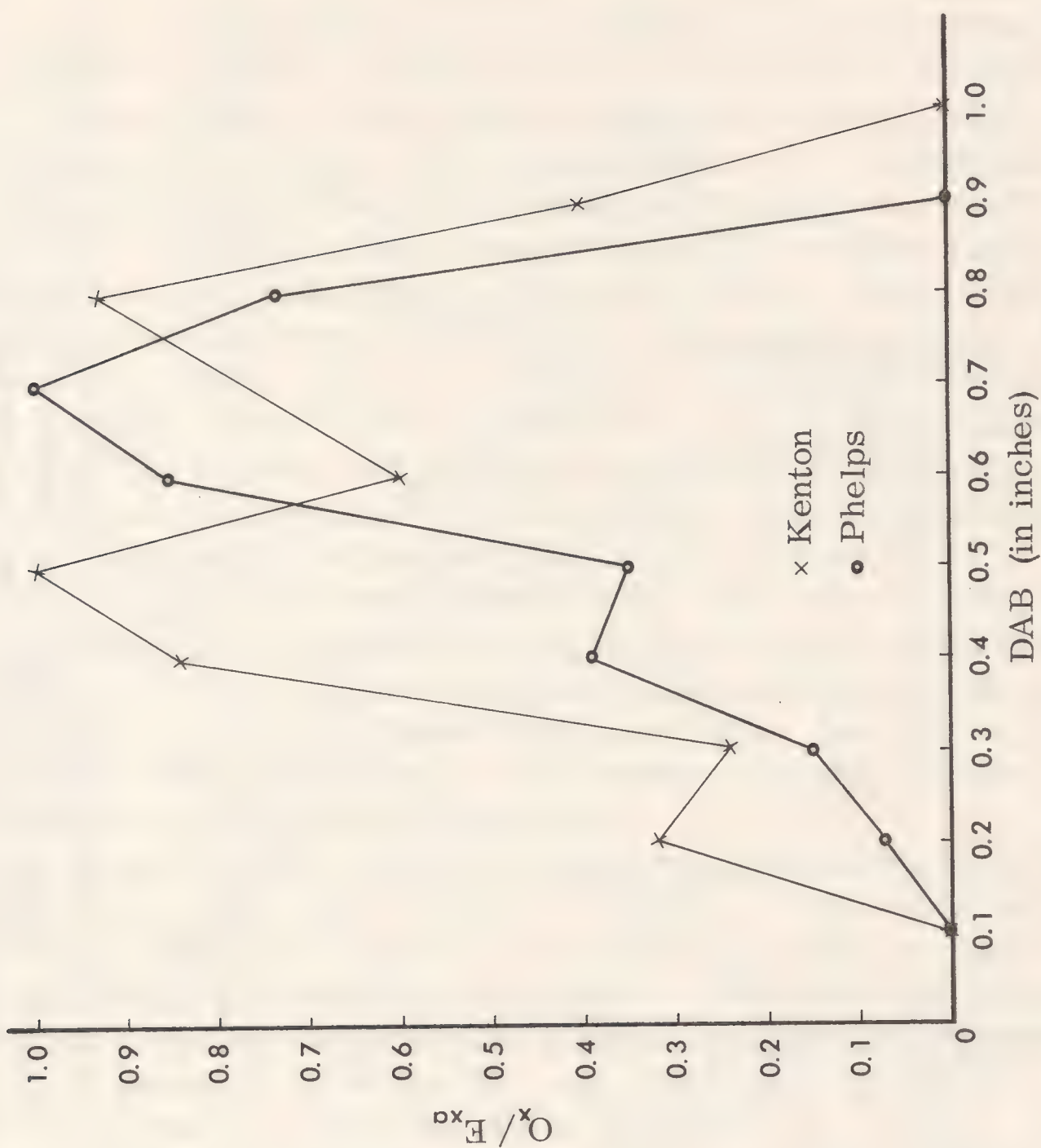


Fig. 24. Distribution of Agrilus hornei eggs: ratio of the observed (O_x) and adjusted expected numbers (E_{xd}) of egg-bearing suckers for each sucker DAB (diameter at base) category plotted as a function of sucker DAB.

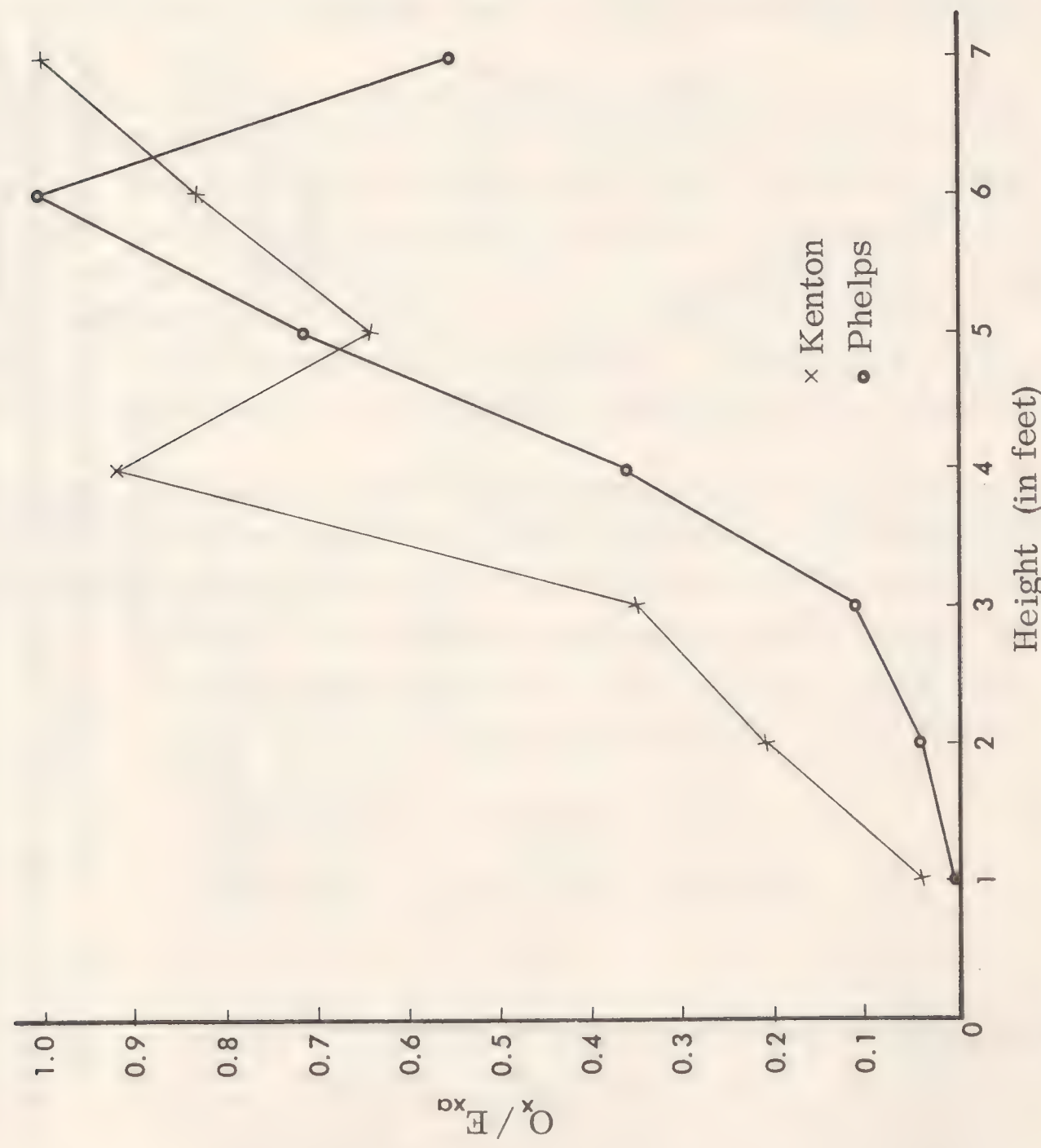


Fig. 23. Distribution of Agrilus hornei eggs: ratio of the observed (O_x) and adjusted expected numbers (E_{xd}) of Egg-bearing suckers for each sucker height category plotted as a function of sucker height.

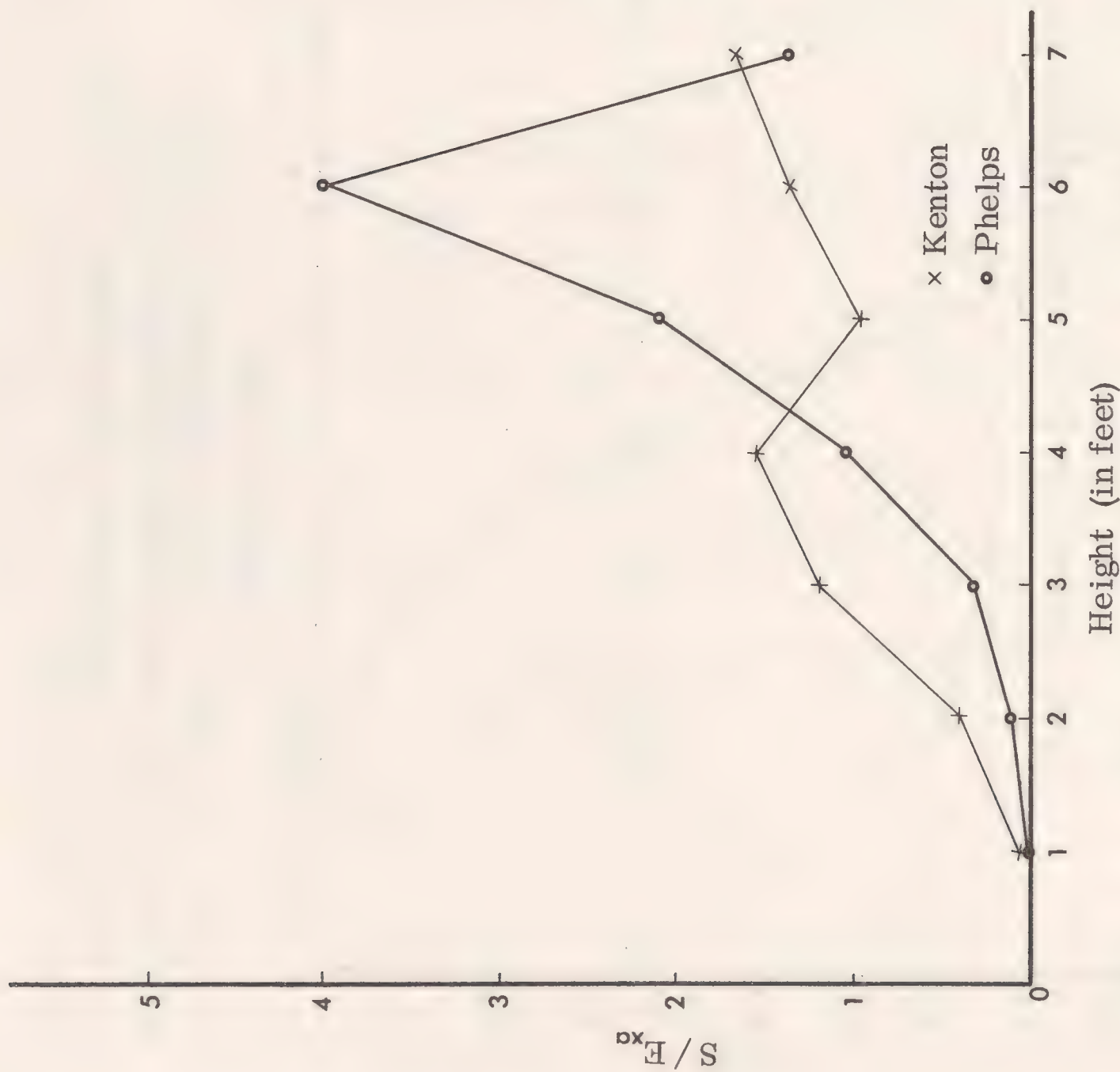


Fig. 25. Total Agrilus horni eggs (S) found on egg-bearing suckers of each height category, divided by the adjusted expected numbers (E_{xd}) of egg-bearing suckers per category and plotted as a function of sucker height.

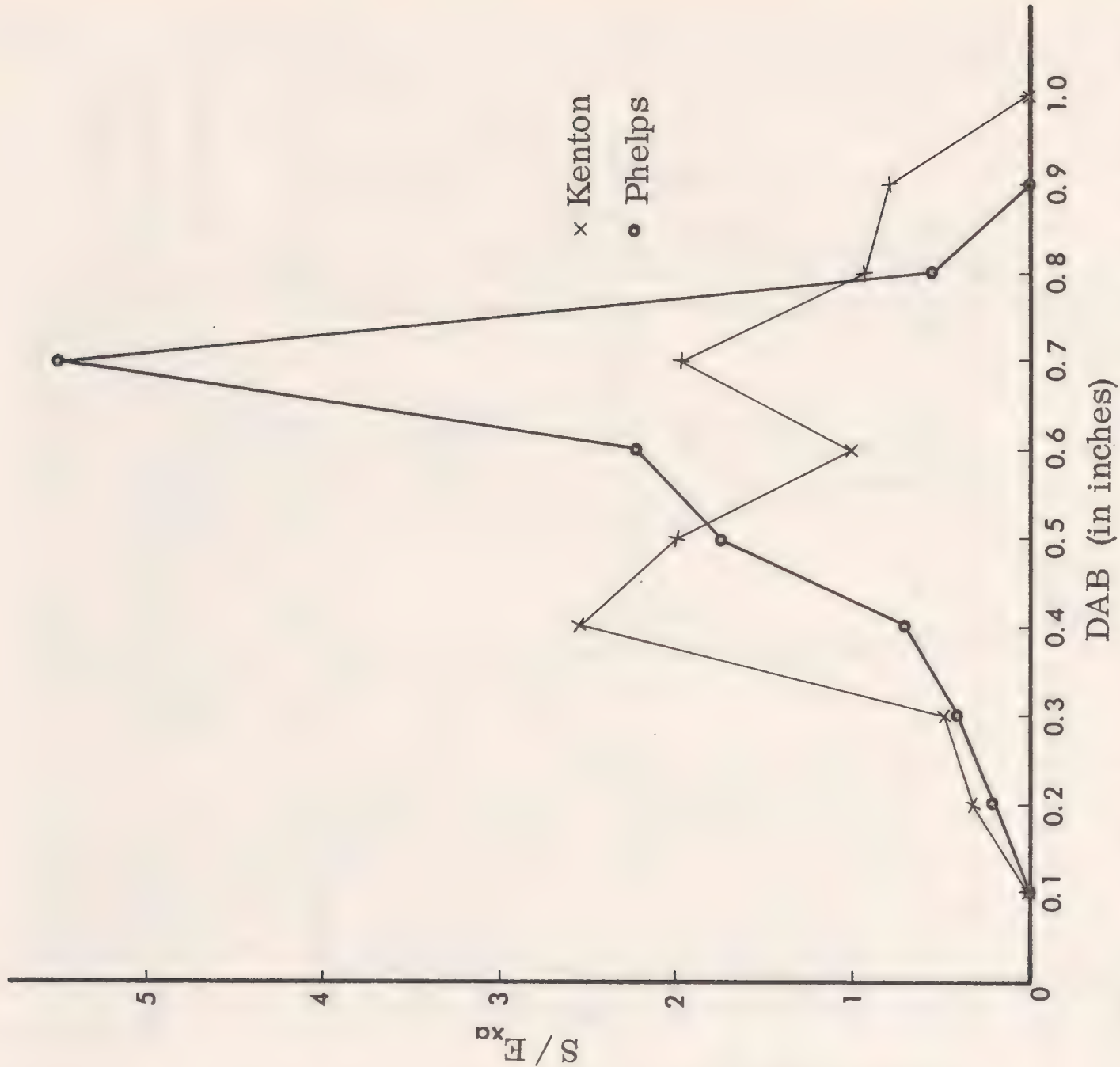


Fig. 26. Total Agrilus horni eggs (S) found on egg-bearing suckers of each DAB (diameter at base) category, divided by the adjusted expected number (E_{xd}) of egg-bearing suckers per category and plotted as a function of sucker DAB.

Without data on the DAB frequency distribution of a stand to compare with that of its egg-bearing suckers, one probably would not come to the same conclusion. In other words, the information obtainable by sampling at random in respect to sucker size and tallying only data pertinent to egg-bearing suckers would be quite different from that presented above. Hypothetical numbers of egg bearing suckers for Phelps and Kenton are plotted in figure 27a, and represent what might have been expected from a random sample of 1000 suckers in each area, as calculated by Carlson (1968). Figure 27b shows that 2/3 of the egg-bearing suckers in the Phelps area would probably have been below 0.4 inches DAB, while a like proportion for the Kenton area should have been below 0.5 inches. Figure 27a agrees with a priori expectation for a random sample in that the curves are negatively skewed and have less pronounced maxima than those in figure 25. The negative skewedness of the former is due to the preponderance of suckers of smaller sizes (the "j" age-frequency distribution). A possible explanation for the disparity between the two curves is that horni tends to oviposit on suckers that may be somewhat above optimum size for survival of larvae as a natural compensation for the preponderance of suckers which possibly are below optimum size. A study of the relationship between sucker DAB, root size, and survival of horni larvae would, of course, be necessary for proving this hypothesis.

The mechanism which restricts horni egg placement to suckers within moderately narrow diameter limits is unknown, but it may be proprioceptive. Proprioceptors that could operate in measuring suckers could be located in the legs, antennae, or even the ovipositor. There are no obvious morphological features differing from those of either anxius or g. liragus that could be singled out as possible sites for the supposed proprioceptors. However, horni varies much less in size than either anxius or g. liragus, and the genetic basis for this lower variability may not be unrelated to horni host selection behavior.

In reference to horni, Graham et al. (1963) say that "the root-girdling Agrilus deposits its eggs on the bark either near the ground or sometimes a foot higher." Three inches above ground line is the maximum height at which we have found horni eggs under natural conditions. In fact, we found 150 eggs below the 1 inch level, while encountering only 34 above it, a highly significant statistical difference from the expected (table 7). All but 2 of the latter (table 8) were below the 2 inch level. Therefore, Graham et al. (1963) were probably mistaken in identifying anything at the 1 foot level as horni eggs.

The horni eggs were commonly deposited on rough bark (lenticels, cracks, flakes, etc.) against adventitious buds, against or beneath the leaves and stems of mosses which sometimes grow on the bases of the suckers (table 8). Oc-

Table 7. Chi-square comparison of the number of Agrilus horni eggs above and below the 1 inch level on the bases of Populus tremuloides root suckers.

Height above Ground (inches)	Number of Eggs		
	Observed	Expected	χ^2
0-1.0	150	92	36.56
1.1-3.0	34	92	36.56
Total	184	184	73.22**

**Statistically significant at the 0.01 probability level.

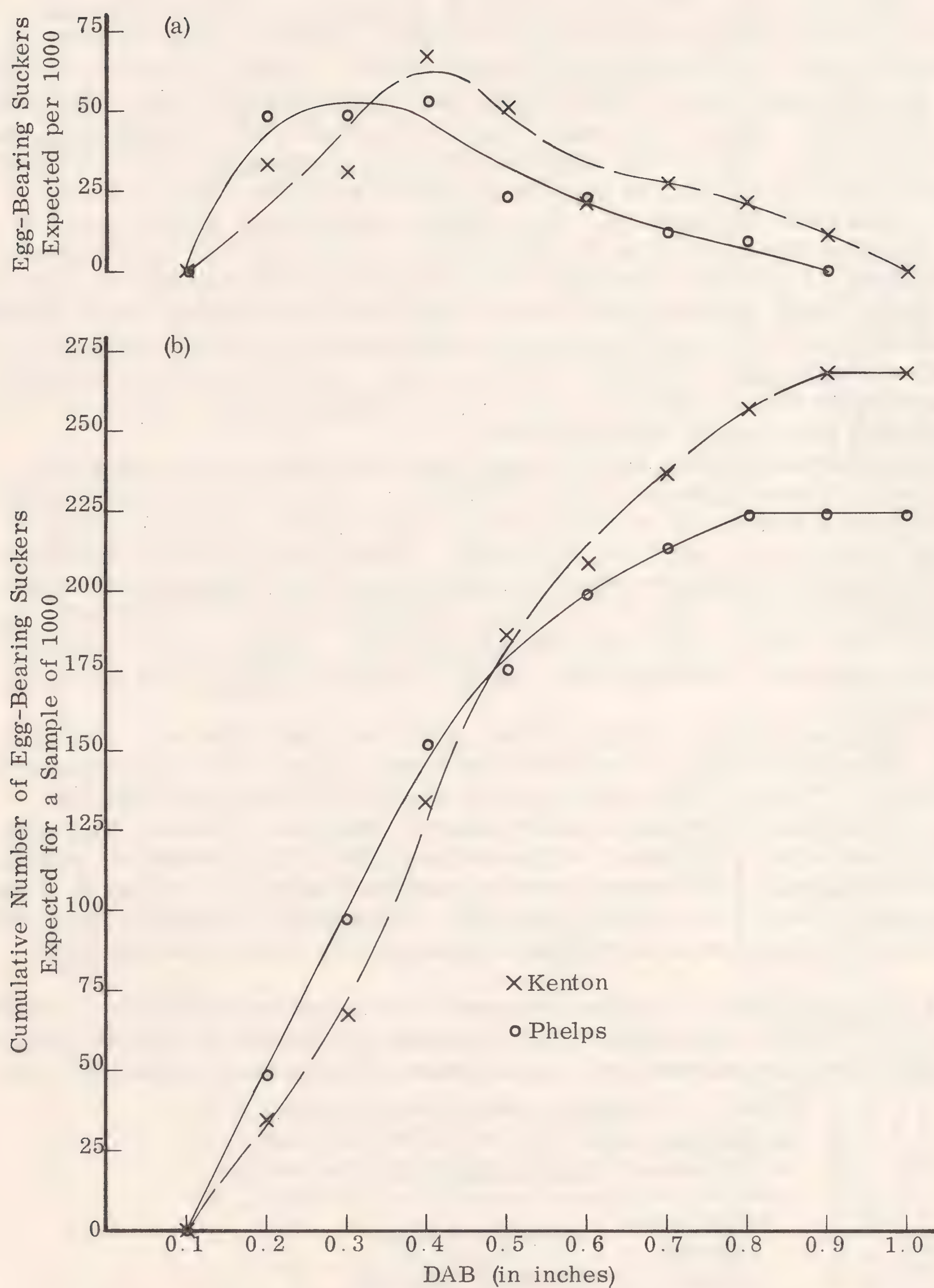


Fig. 27. Hypothetical distributions for *Agrilus horni* eggs: the number of egg-bearing suckers (a) and cumulative number (b) expected for random samples of 1000 *Populus tremuloides* suckers for areas near Kenton, Michigan (dashed line) and Phelps, Wisconsin (solid line).

Table 8. Position and situation of *Agrilus horni* eggs on *Populus tremuloides*: pool of data for 1964 (Beechwood area) and 1965 (Kenton and Phelps areas).

Height Above Ground (inches)	Eggs Situated on or Against:				Total
	Smooth Bark	Rough Bark (flakes, etc.)	Buds	Moss	
0	18	27	13	16	74
0.1 - 1.0	6	43	16	11	76
1.1 - 2.0	1	19	11	1	32
2.1 - 3.0	0	0	2	0	2
Total	25	89	42	28	184

casionally, they were also found on smooth bark, but most of those eggs were located at ground line where they had probably been partially supported by organic debri of some sort. A chi-square comparison between the height distribution of eggs laid on smooth bark and that for all other eggs shows them to differ significantly (table 9). While the number of eggs laid on smooth bark above ground line is less than the expected value, the reverse is true for the number observed at ground line.

Table 9. Chi-square comparison of positions of *Agrilus horni* eggs on smooth bark with positions of other eggs (pooled data from Beechwood, Kenton, and Phelps areas).

Height Above Ground (inches)	Number of Eggs					χ^2
	Observed		Total	Expected [†]		
	Smooth Bark	Other		Smooth Bark	Other	
0	18	56	74	10.06	63.94	6.27
0.1 - 1.0	6	70	76	10.33	65.67	1.81
1.1 - 2.0	1	31	32	4.35	27.65	2.58
2.1 - 3.0	0	2	2	0.27	1.73	0.27
Total	25	159	184	25.01	158.99	10.93*

[†]Expected = (observed column total ÷ grand total) × row total.

*Statistically significant at the 0.05 probability level.

Mating Behavior

FUNCTIONAL MORPHOLOGY

Aedeagus. Before entering the discourse on the behavior of individuals during courtship and mating, it will be necessary to describe some anatomical structures important in mating. Basing the interpretation on Lindroth and Palmén (1956), the aedeagus (fig. 28) of buprestid males is composed of an eversible penis (pe), which is sheathed by the tegmen. The tegmen is composed of the paired parameres (pa) and an unpaired basal piece (bp). The junction between the basal piece and the parameres is not evident in Buprestidae. Hence, the term parameres will be used to denote the part of the tegmen which is divided, the part often called the lateral lobes in buprestid taxonomic discourse. The latter, and the associated designation of the penis as the medi-

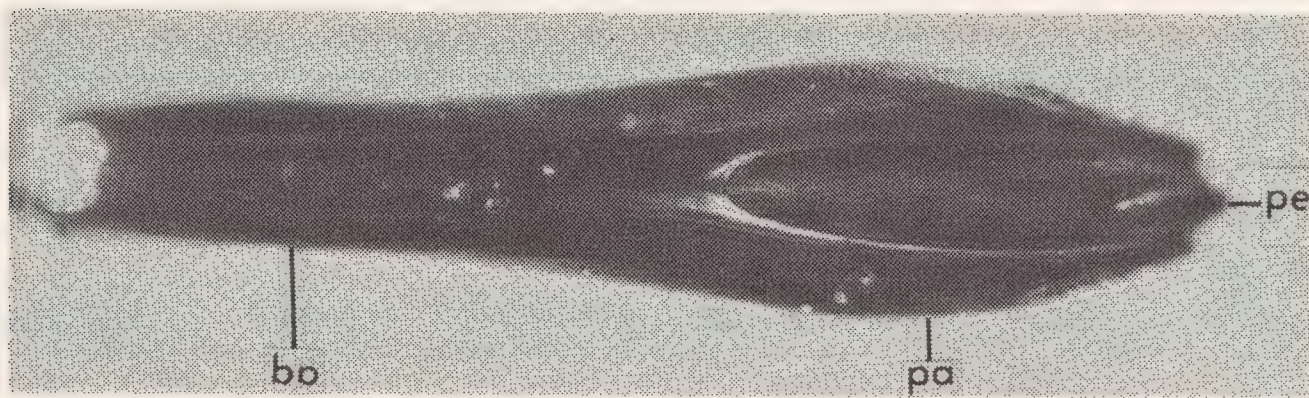


Fig. 28. Dorsal side of the aedeagus of *Agrilus granulatulus liragus*; pe = penis, pa = parameres, and bp = basal piece.

an lobe, are not useful terms for functional descriptions.

On the ventral¹ side of the tegmen (figs. 5-8) of species in the *anxius* group, there is a trough or groove which extends from near its base to the tips of the parameres. It is very narrow at the base of the tegmen and gradually increases in breadth toward the apex, broadening most in *anxius*, but much less in *horni*. During coitus this groove receives the pygidial spine of the female, which serves to guide the aedeagus into position. The groove also appears to have functions connected with sexual recognition which are discussed later.

There is also a groove on the dorsal side of the aedeagus (fig. 28), although it is rather shallow in comparison to that on the ventral side. The penis is only slightly recessed below the dorsal surface of the parameres, which are rather flattened, and the groove extends basad of the parameres, sometimes nearly to the base of the tegmen.

Movements of the heavily sclerotized aedeagus appear to be controlled mostly by the large muscles that are directly attached to it. The ovipositors of buprestids, on the other hand, are not heavily sclerotized. As there are no muscles directly attached to them, they are principally hydrostatic organs.

Female Organs of Reproduction. The only interpretation of the morphology of a buprestid ovipositor known to us is that of Tanner (1927). Because the ovipositors of Buprestidae appear to differ from those of other Coleoptera, it seems best to employ his interpretation. After the homologies are worked out, it may be possible to use less burdensome terminology.

The ovipositor of species in the *Agrilus anxius* group (fig. 29) differs from the configuration shown by Tanner (1927) for *Chrysobothris debilis* Leconte in a single important way. The *C. debilis* ovipositor, which is similar to that of a *Buprestis* sp., has the bacula of the proctiger and coxite separated by the entire length of the valvifer baculum. Species in the *A. anxius* group have the bacula of the proctiger and coxite separated only by the thickness of the valvifer baculum. The valvifer baculum lies beside that of the coxite, and the two are nearly parallel, except at their bases, where the valvifer baculum intervenes between the bacula of the coxite and proctiger.

Figure 29 shows the *Agrilus anxius* ovipositor in its various attitudes. A comparison between fig. 29, c and d shows how the ovipositor can be likened to a tube within a mostly membraneous sac. The part of the ovipositor bearing in the coxites will be referred to as the ovipositor tube. It appears that only this part of the ovipositor is actually extended from the abdominal cavity during oviposition.

During copulation the male aedeagus is inserted to the point where the tip

¹Ventral in the retracted position, as is traditional; not ventral *sensu* Lindroth and Palmén (1956).

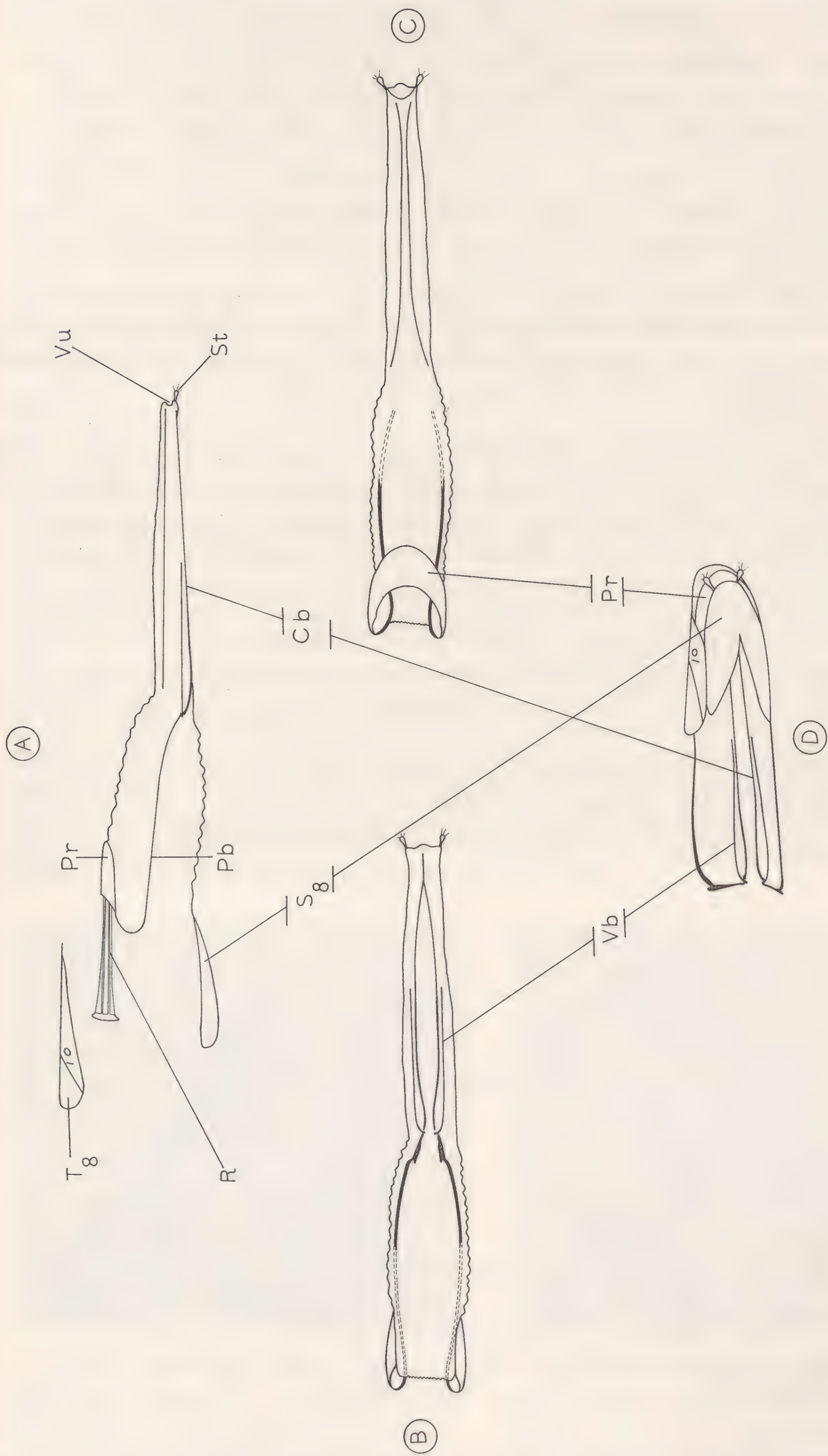


Fig. 29. Lateral (A), ventral (B), and dorsal (C) aspects of the ovipositor of *Agrilus anxius* in extended position (about X20). The degree of extension shown in A through C simplifies the illustrations, but ovipositing females do not appear to extend the ovipositor as completely. The view shown in D is ventro-lateral in retracted position. All views were drawn without the aid of a camera lucida. The symbols: T₈ = tergite 8, S₈ = sternite 8, R = rectum, Pr = proctiger, Vu = vulva, St = stylet, Pb = proctiger baculum, Vb = valvifer baculum, and Cb = coxite baculum.

of the female's pygidial spine rests in the basal end of the ventral groove on the tegmen. When the aedeagus is in this external position, its probable internal position in relation to the various bacula of the ovipositor tube is as shown in fig. 30. It is assumed that after this position is attained, the male everts the penis into the vagina (Va, fig. 31). The tip of the penis probably fits into the receptacle (Rp, fig. 31). The wall of the vagina has a complex, thickened structure which gives it great elasticity. It is therefore assumed that after the penis apex enters the receptacle, eversion of the penis continues until it is fully extended. It appears that the elasticity of the vagina may allow successful interbreeding between even the individuals at opposite size extremes in populations with extensive size variation.

After the penis is fully extended, the internal sac is evidently everted upward into the bursa copulatrix (Bc, fig. 31). The minute spinules surrounding the opening to the bursa apparently guide the sac into place. They probably also serve to hold the sac in place as insemination occurs.

BEHAVIOR OF MALES

Sexual Recognition. When a male (A)¹ mounts another individual (B), he almost immediately exserts his aedeagus, which at first projects backward, but then rotates downward and forward such that its apex contacts the tip of the abdomen of individual B. After the abdomen of B is contacted, the subse-

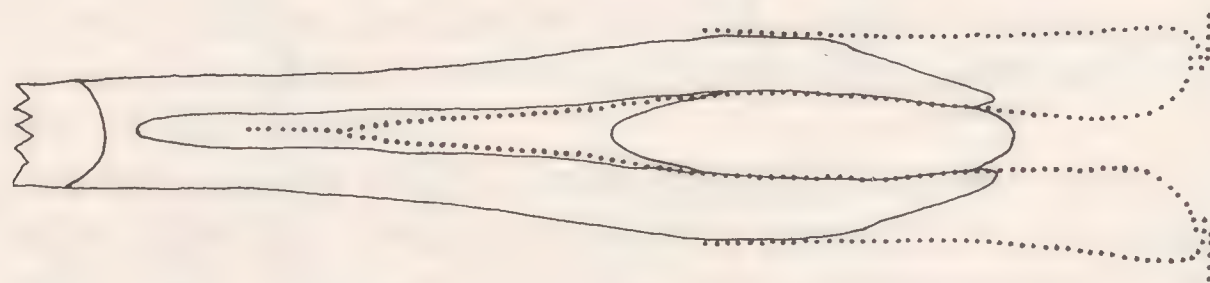


Fig. 30. Probable position of the dorsal side of the aedeagus (solid line) relative to the bacula of the ovipositor (dotted line) during copulation in *Agrilus granulatus liragus* (cf figs. 28 & 29).

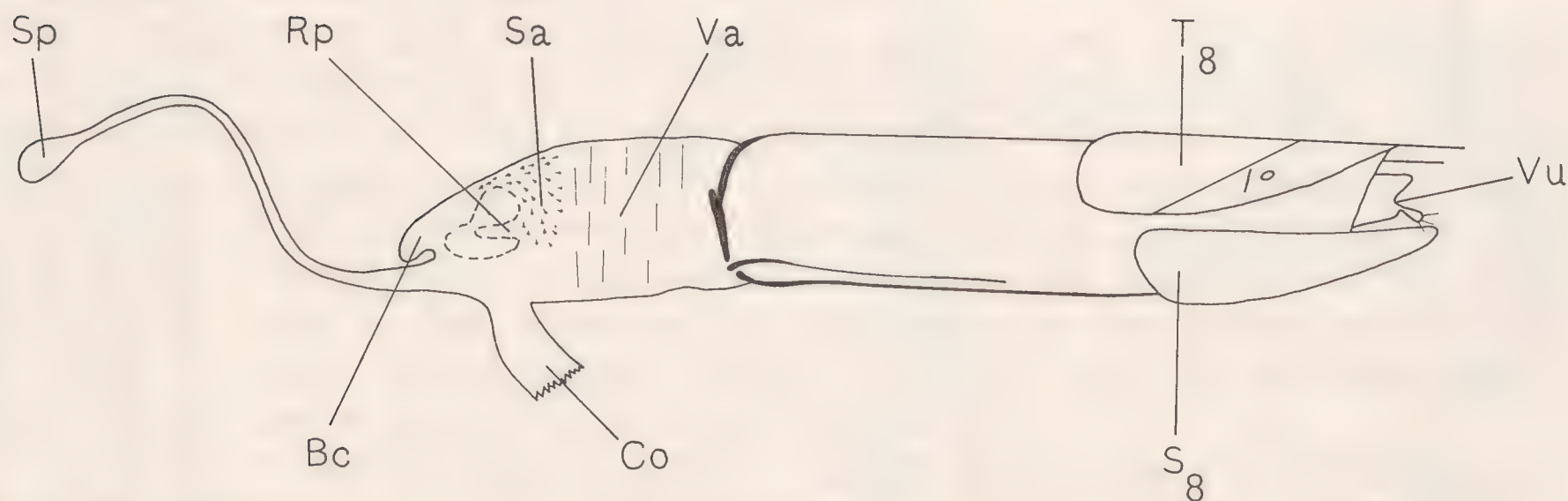


Fig. 31. Lateral view of the *Agrilus anxius* ♀ internal organs of reproduction (less ovaries) and ovipositor (retracted position); Sp = spermatheca, Rp = receptacle for penis apex, Bc = bursa copulatrix, Sa = spiculate area of vagina, Co = common oviduct, Va = vagina, T₈ = tergite 8, S₈ = sternite 8, and Vu = vulva. Drawn without the aid of a camera lucida.

¹Hereafter courting males are referred to as "A" and the individual being courted as "B."

quent behavior of the courting male (A) depends upon the position of the hind sternite of individual B. If the sternite is in lowered position, insertion and copulation ensue, provided B is a female. If B is a male, the tips of the aedeagi of both come into contact and male A dismounts quickly.

When the aedeagus dissected from a male was placed into the abdominal opening of virgin females, courting males responded to them just as they did to males, provided the aedeagus artificially implanted in the females had not moved to the side of the abdominal opening. Therefore, it appears that the responses of courting males are elicited by what they touch with the aedeagus. The observations were few, however, and only one observation was made on a male courting another whose aedeagus was removed. In this case insertion of the aedeagus occurred, and when the behavior of male A indicated that he was everting the internal sac, he was removed, whereupon the sac was revealed protruding from the tip of the penis.

When a courting male probes an individual not having the hind sternite in lowered position, the process of sexual recognition is somewhat more intricate. Before the behavior of courting males in this situation can be described, some sexually dimorphic structures of the last abdominal segment must be discussed. The role played by the female pygidial spine during insertion of the aedeagus has already been partially considered. Were this the only function of the spine, it would be difficult to explain its presence in males. Moreover, male pygidial spines are often somewhat longer (relative to body length) than those of females. The significance of this dimorphism seems to relate to the function of other sexually dimorphic structures of the hind segment. In both sexes the marginal sclerite of this segment is smooth and flattened, and a groove separates it from the sternite. The apex of the hind marginal sclerite of females is angled slightly upward, or beveled, with respect to the sternite (fig. 32). In males, however, its apex lies in almost the same structural plane to which the sternite conforms (fig. 33). The groove between the marginal sclerite and the apical part of the hind sternite seems to be somewhat larger in females than males, but this appears to be partly due to the differences in the angulation of the marginal sclerite.

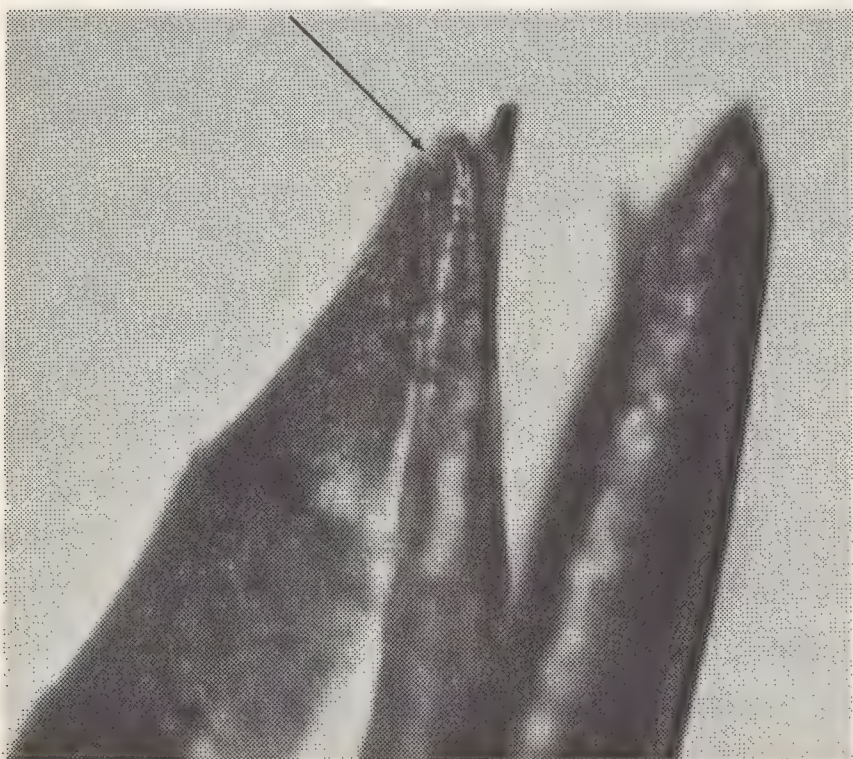


Fig. 32. Abdominal apex of Agrilus granulatus liragus ♀; arrow points to the groove between the marginal sclerite and sternite of the last segment.

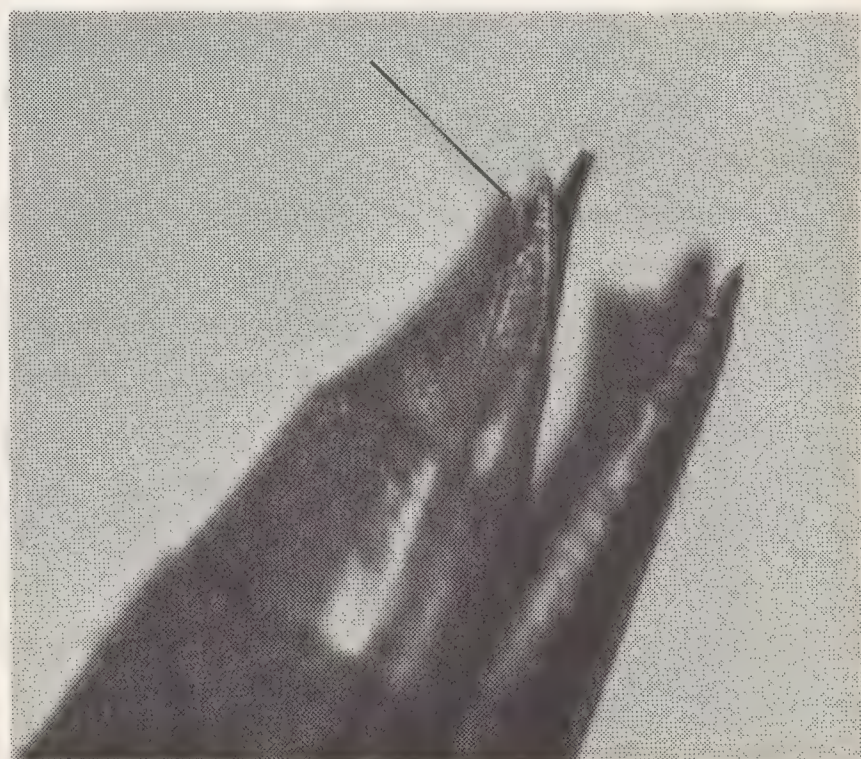


Fig. 33. Abdominal apex of Agrilus granulatus liragus ♂; arrow points to the groove between the marginal sclerite and sternite of the last segment.

Let us return to the situation in which a male probes an individual whose hind sternite is in the closed position. The tip of the aedeagus of A first touches the marginal sclerite of B at or near the point where it closes against the pygidium. After this point is contacted, A draws the proximal portion of the aedeagus upward. This causes its tip to move ventrally, since the pygidial spine of B acts as a fulcrum, fitting in the ventral trough of the tegmen about midway along the parameres. When the tip of the aedeagus moves downward and forward it comes into contact with B's sternite. When B is female, the sternite resists the downward movement of the aedeagus, as the latter catches in the groove between the marginal sclerite and sternite. On the other hand, if B is male, the groove fails to catch the tip of the aedeagus, which slips freely past. This appears to be due to the combined features of the apical marginal sclerite and the pygidial spine of male B.

When males are probed, dismounting is the only outcome. This is elicited either when a probing male's aedeagus slides past the groove between male B's marginal sclerite and sternite or when its aedeagus contacts that of B. The probing of females, on the other hand, has several possible outcomes, depending upon her receptivity. Immediate insertion of the aedeagus occurs when B has her hind sternite already lowered prior to probing, but when it is not, the prying movement of A's aedeagus may lower it, provided B is a receptive female. If she is not, a male may be unable to insert its genitalia, and will persist in probing until (1) coitus is achieved, (2) he is knocked free of B as a result of her "frenzied" scurrying, or (3) until he fatigues (or appears to fatigue).

The hypothesis that sexual recognition by males is chiefly a physical process was tested in the laboratory by altering the structure of the last segment in both sexes with glue. Some evidence was obtained in support of the hypothesis, as the attempt to create a female-like male was partially successful. Males behaved quite differently after mounting and probing altered males than they did when courting normal males. All of the results obtained at first did not seem consistent with the hypothesis, but it was discovered subsequently that consistent results cannot be expected unless the last segment of an altered male is held tightly closed. After this was taken into account, the results were less variable. Some males then mounted and probed altered ones several times in succession before dismounting. Others continued probing for up to 5 minutes.

Physical contact definitely plays an integral part in sexual recognition by males. The important question that remains unanswered seems to be this: when a female holds the hind sternite in closed position as she is mounted and probed by a male, is the response of the male dependent entirely upon physical contact or does he receive some additional stimuli (e.g. chemical) which work in combination with the physical ones? If attempts to modify the structure of the hind sternite of females had not failed completely, a more definite answer to this question might have been possible. Unfortunately, the minute size of the crucial structures makes it impossible to smooth them over with glue or similar substances, like those used to modify the structure of the hind sternite in males. The mass of the applied material inevitably produces a bump which is more of an obstruction to the aedeagus than the groove between a female's hind marginal sclerite and sternite. Other means must be found to smooth over this groove and there must be more tests carried out with females that have an excised male aedeagus implanted in the opening to the abdominal cavity. The small amount of evidence obtained by the latter technique seems

to indicate that males may not recognize females by means alternative or additional to the physical ones.

Insertion of Aedeagus and Insemination. After insertion of the aedeagus is initiated the female pygidial spine apparently continues to play a significant role for successful coition. It continues to act as a fulcrum while the male alternately lifts the proximal part of the tegmen and then pushes the aedeagus into the ovipositor tube (fig. 34, 39c). These movements by the male seem to assist insertion by putting pressure against the female's hind sternite to push it downward, and the sheath-like lower part of the ovipositor tube is probably simultaneously pulled away from the fleshy upper portion.

When full insertion of the aedeagus is achieved (fig. 39d), the male's hind sternite is nested in the notch between the tips of the female's elytra, while her pygidial spine rests in the proximal part of the ventral trough of the aedeagus.

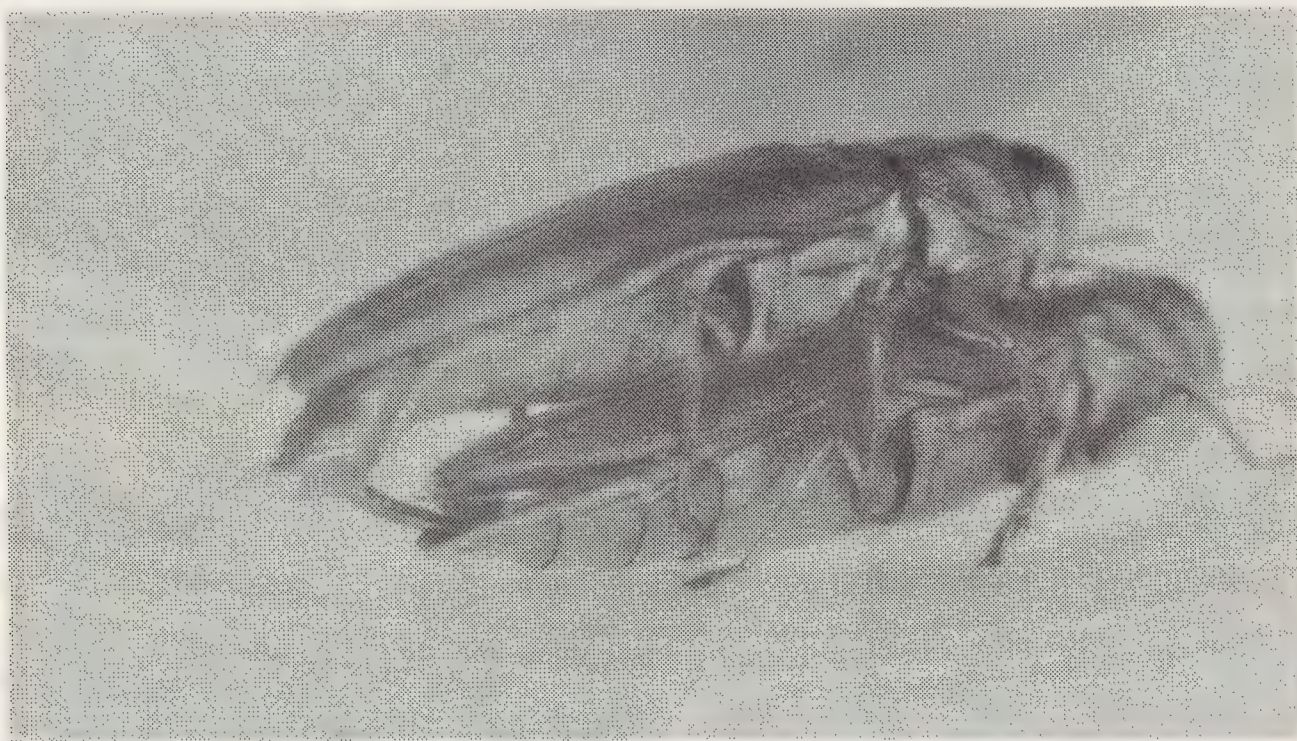


Fig. 34. Mating of an *A. anxius* ♂ and an *A. granulatus liragus* ♀. The aedeagus is being pushed into the ovipositor tube (not visible) following the prying of the last sternite away from the pygidium. This downward prying occurs when the male raises the abdomen, which brings the median part of the aedeagus into contact with the pygidial spine of the female, which acts as a fulcrum.

gus (which faces dorsally in the inserted position). After several minutes the male begins a series of vibrant movements, at which time the middle and hind legs are usually extended laterally. Eversion of the internal sac probably starts with commencement of these movements, because males removed from females during this phase of coition had the internal sac partly everted, protruding from the gonopore. Males removed somewhat later lose the internal sac which is apparently restrained by the spinules around the opening to the bursa.

Behavior of Males Under Natural Conditions. Information about *Agrilus* spp. suggests that they depend upon host selection, at least in part, to bring about the meeting of the sexes. In other words, the kind of site utilized for mating by a particular species depends on many of the same factors which govern the selection of sites for oviposition. Therefore, these are also the factors which

prevent interspecific matings from occurring, while making it quite likely that intraspecific pairings do occur.

Bronze Birch and Bronze Poplar Borers. Excepting the host specificity factors, the mating behavior of anxius and g. liragus is similar. For efficiency in making observations, most field work on the mating behavior of these species involved watching individuals which were on wind-falls (fig. 35), logs, or logging slash (fig. 36). It is fairly safe to assume that they do not behave very differently on these hosts than on upright ones.

The males of g. liragus and anxius move along the stems of their hosts, usually remaining still for only brief but frequent interludes. On very warm days, the movements of these beetles are rather rapid and the hesitations are very brief, so that they move rather continuously with a jerky motion. On cooler days they remain stationary for rather long periods, and are not conspicuous. These insects are not active at temperatures below 70° F (Barter 1957, 1965).

When any arthropod passes within a foot or so of these Agrilus males, the males approach the former. If the other animal, in turn, approaches them aggressively, such as was observed with ants and males of a larger buprestid, Chrysobothris sp., the Agrilus male responds by releasing its grip on the host and falling free of it. However, if the other arthropod is moving away from the Agrilus, the latter pursues. In one instance a g. liragus male was seen following a Dicerca (another buprestid), and upon overtaking the latter, the g. liragus male actually scurried part way up onto the elytra of this much larger insect.

When two anxius or g. liragus males approach each other, they usually do so more gradually, at least if each has detected the other, which usually is the case. After the males stand facing each other from a distance of one to several inches, one of them quickly approaches and mounts the other. Such homosexual encounters occur very frequently in nature, much more frequently than heterosexual ones. They may have a special significance, particularly for anxius and g. liragus.

Homosexual encounters seem to have a survival value that is real. A. anxius and g. liragus males exhibit a sort of quasi-territorialism on their hosts. After a male mounts and probes another, he usually flies or walks to a different part of the host. These encounters between males seem to have an interesting uniqueness in that it is the aggressive male that is usually repelled. There is nothing to indicate that the aggressor can be repelled by anything short of mounting and probing. The seemingly inefficient means by which the males of these Agrilus recognize each other may be important in keeping them spatially separated. This quasi-territorialism among males may serve to increase the probability of occurrence of heterosexual encounters.

The beneficial effects of homosexual encounters may not be derived without some cost to the sexual responsiveness of the aggressive male. During laboratory studies of behavior it was discovered that if males are removed from females just after completing the sexual recognition phase of courtship and are immediately released again, they often mount the next individual they encounter (either sex). The sexuality of males is definitely enhanced when they mount and probe females, and it is apparently not greatly diminished by artificial termination of courtship. However, males whose sexual responsiveness has been enhanced in this way, seem to lose it after a short sequence of homosexual encounters. Perhaps the decrease in sexual aggressiveness occurs as an integral part of the reaction which causes an aggressive male to move away from the one he has mounted.



Fig. 35. Populus tremuloides windfall, typical of those where the adult behavior of Agrilus granulatus liragus was observed.



Fig. 36. Betula papyrifera logging slash, a typical observation site for the studies of the adult behavior of Agrilus anxius.

Apparently, there is some sort of threshold which must be reached before courtship is elicited in males, and when that threshold has been reached or exceeded, males court immediately upon encountering other individuals. All males on their hosts under natural conditions seem to have high sexual responsiveness. This indicates that factors associated with their attraction to mating sites and their pre-courtship behavior may induce this responsiveness.

During their vigil on the host, anxius and g. liragus males are often observed repeatedly exerting the aedeagus. This behavior is also exhibited in the laboratory by males not on their hosts, and it seems to occur well in advance of the attainment of the mating threshold. It could be a antagonistic aspect in a part of the male behavioral repertoire that is somewhat self-regulated as a balance between antagonistic and antagonistic aspects. The existence of this kind of behavioral balance has been demonstrated in other groups of insects (see Kennedy and Booth, 1963; Graham, 1959, 1961).

Little has been established concerning the extent to which the energy of females, once they have reached the host, is spent in activities which lead to encounters with males. Most field observations seem to indicate that they are rather passive. On the other hand, laboratory studies of mating indicate that females may court males. On a number of occasions, virgin g. liragus females mounted males and displayed many of the actions typically manifest by males in courtship. In some cases the ovipositor was even exerted. Virgin anxius females never showed such a striking "maleness", but occasionally they moved part way up onto the elytra of males and flailed the antennae in the manner of courting males. Whether or not virgin females would show the same sort of response to other females is not known. No such behavior was ever observed in the field, and must happen only rarely, if at all. Moreover, under natural conditions, males seem to most readily mount individuals which turn away from them. It is difficult to reconcile this with active courtship by females, unless it is natural for the sexual aggressiveness of females to be subordinated by that of advancing males, with females terminating their courtship by turning away from males.

According to Barter (1965) g. liragus males "actively seek or ambush non-ovipositing females." He says that ovipositing females are unattractive to males, but this does not appear to be an entirely accurate statement. Barter observed mating less frequently between 1:00 and 4:00 PM, the peak hours of oviposition. This alone does not show that ovipositing females are unattractive to males, however. Males simply do not encounter ovipositing females frequently. Females ovipositing on logs are found along the sides of the logs on days when the males orient more to the upper surface. Ovipositing females are, therefore, usually not within the line of sight of males.

Because females are motionless while eggs are being deposited, males are not likely to detect them then. However, ovipositing females are approached by males which detect them moving between egg deposition sites. One ovipositing g. liragus female under observation was approached by two males. After moving away from the first male, she was encountered by the second. Although she also moved away from the latter, he overtook her and mounted. The female stopped moving only after the male had inserted the aedeagus, after which copulation proceeded normally. Therefore, ovipositing females are not unattractive per se, although they may be rather unreceptive to courting males.

Laboratory observations indicate that females courted after having recent-

ly mated are particularly unreceptive. When females are totally unreceptive, courting males are usually unable to insert the aedeagus. It appears that total unreceptiveness occurs only after insemination occurs. When males are removed from females during the course of mating and prior to insemination, the females are usually receptive to the next male to court them.

The Aspen Root Girdler. Although g. liragus and anxius are provided with a means for meeting of the sexes which apparently depends upon odors coming from bio-chemical degradation of the host, horni mating is brought about through more subtle means. A. horni males are apparently able to select hosts of a favorable physiognomy and in such ecological situations that the chances for encounters with females are enhanced, but it hardly seems as certain a means as that common to anxius and g. liragus. There is a possibility that horni males or females emit air-borne sex attractants. There is no evidence to suggest that this is the case, however. A. horni males merely seem to orient to poplar suckers which females are likely to land upon. They sit on the sucker stems, facing upward, and their position usually ranges from near the ground to near the point where the sucker's lowest side branches are produced, a height of about one to three feet. The males stay in nearly the same position for periods averaging about 15 minutes, during that spell usually moving only when another arthropod moves near it on the stem. After such a period, they move upward and out onto the leaves to feed for one to several minutes before resuming their vigil on the stem. One male remained on the same sucker for more than 2 1/2 hours, but this may be an exceptionally long stay.

The entire horni courtship and copulation was observed only once in the field. In that case, as the female came down the sucker stem and neared the stationary male, he, in turn, approached her. The female then flew, but landed again on the foliage of the same sucker, while the male moved rapidly to the base of the sucker and turned upward. The female came down the stem again, and when she was approached by the male she turned upward. The male moved up quickly from below and mounted. After they had been in copulo for about 15 minutes, the female crawled up the stem and onto a leaf where the male dismounted. In one other instance in the field, the last part of horni copulation was seen, and it terminated just as in the preceding one. In each case, the female flew to another sucker as soon as the male dismounted.

There is an interesting parallel between these field observations and laboratory observations on horni copulation. In the laboratory, too, the males remained mounted after the females began moving around. In one instance a copulating female which had remained still for 10 minutes, ran about in the petri dish for 24 minutes with the male remaining mounted. In another case, the female remained placid for 17 minutes, but ran about for the remainder of the mating period, which totalled 21 minutes. In a field cage (fig 37), a copulating female which fell from an aspen sucker with the male still mounted, ran about on the ground for 40 minutes before the male was dislodged. The tegmen was partially to fully inserted during the entire 40 minutes. Several times the female seemed to orient towards debris which she could pass beneath, but which would not allow the male to pass freely. It is difficult to believe that the behavioral repertoire of horni females could include such a specialized facet for dislodging males. After it had occurred several times, however, the possibility seemed less remote.

The males of anxius and g. liragus do not usually remain mounted long after the females begin moving about. Barter (1957, 1965) found that the av-

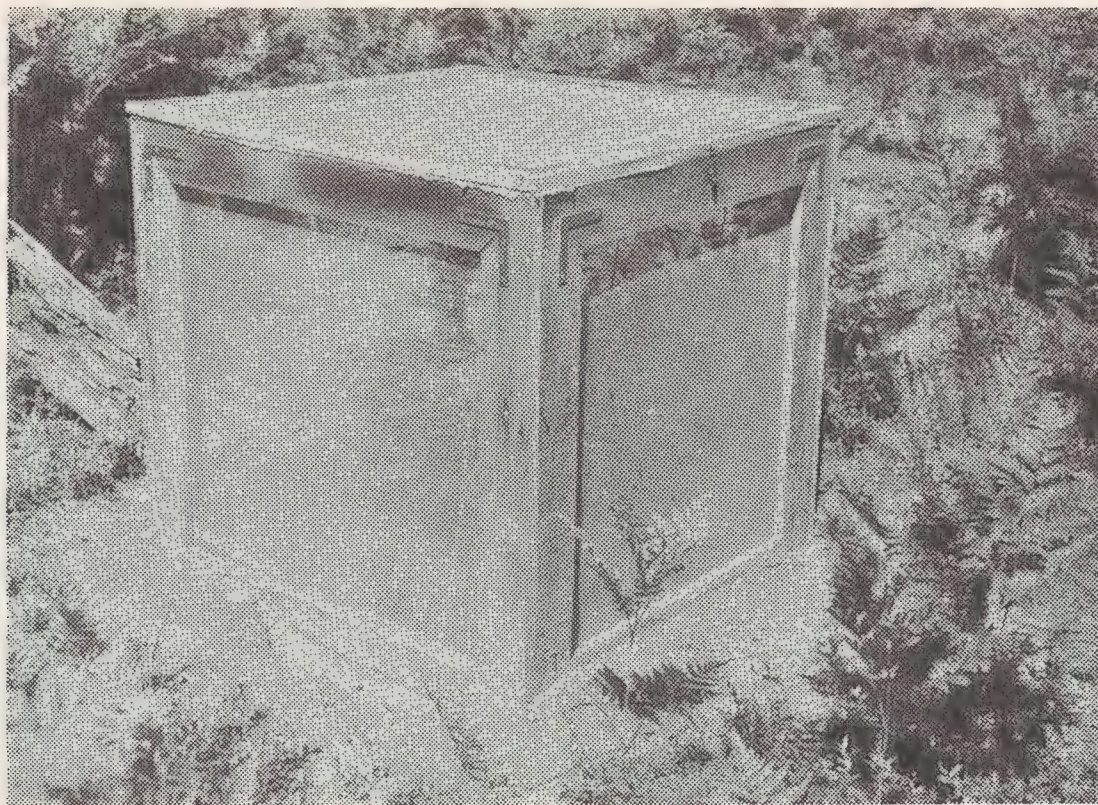


Fig. 37. One of the field cages where some observations on Agrilus horni adults were made. Note that these observations are not those designated in the text as field observations; the latter, comprising the majority discussed, refer to observations on beetles not in captivity.

erage time elapsed in copulo was 7 minutes for anxius and 5 minutes for g. liragus. He says the maximum observed for anxius was 23 minutes.

FEMALE ACCEPTANCE OF MALES. Other species differences in mating behavior were discovered primarily through attempts to obtain interspecific crosses in the laboratory. These experiments showed that the females of Agrilus horni will not mate with g. liragus males. In 43 recorded attempts to obtain this cross, none was successful, as the g. liragus males could not insert their genitalia. Often, these males would remain mounted for extended periods, up to 5 minutes or more, continually probing the hind segment of the horni female.

In 29 recorded attempts to cross anxius females with g. liragus males, only 4 led to copulation. A. pensus females, on the other hand, appear to be receptive to g. liragus males. They are also receptive to anxius males, but may not be receptive to horni males. In a number of attempts to pair horni males and pensus females, the latter usually did not seem to be receptive, and copulation resulted only twice. In one of those cases the pensus female did not seem entirely receptive. The difficulties encountered with the survival of pensus adults abbreviated the testing of this interspecific pairing, and left us with inconclusive results. A. granulatus liragus females are promiscuous, accepting males of any of the four species involved in these tests.

When a male mounts a female, he thrusts his head and prothorax forward and flutters the antennae over her head and the base of her pronotum (fig. 38)¹, and sometimes they are simultaneously drawn back rapidly making a long stroke over the lateral parts of the pronotum (fig. 39). At the same time males palpate the female's pronotum near the depression lying just anterior to the scutellum. Sometimes, males perform these antennating and palpating move-

¹The antennal movements during courtship appear to be the same as those occurring later. Because it is extremely difficult to get the beetles into proper position for photographing during courtship, I am forced to use photographs taken during copulation.

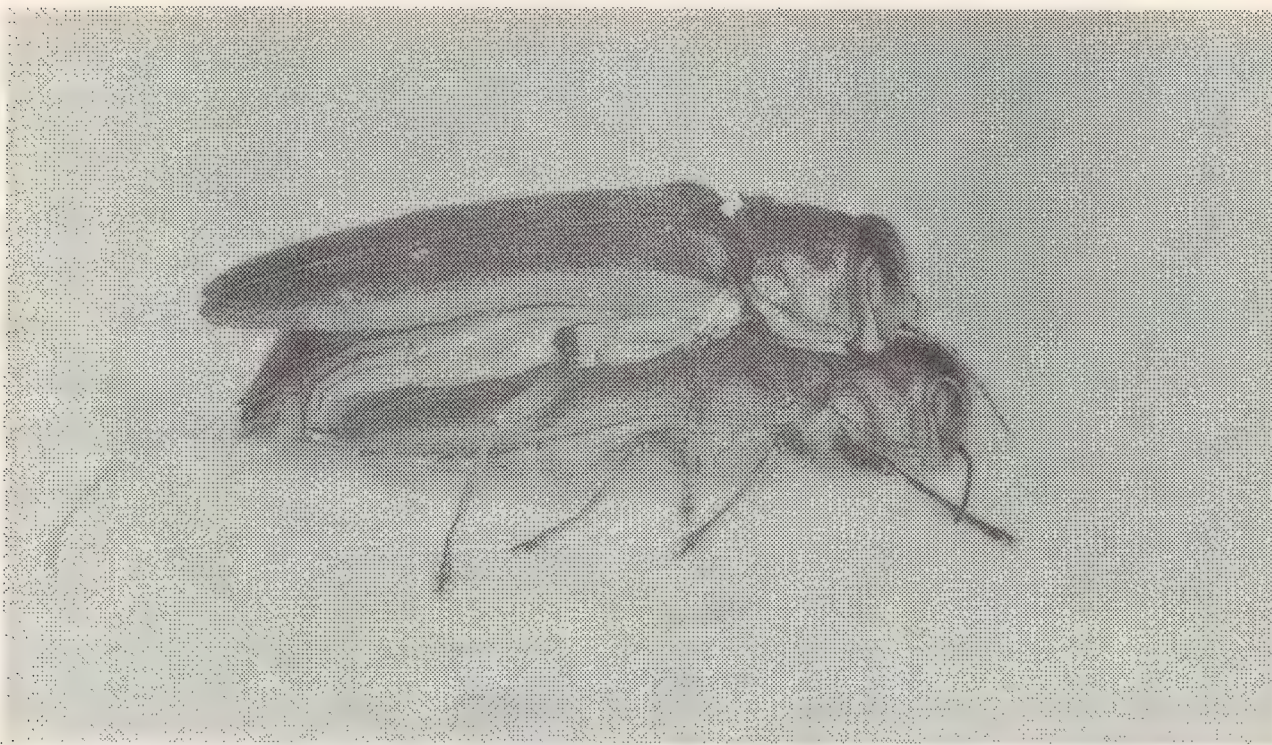


Fig. 38. Position of the antennae at one point during "fluttering" by an *Agrilus anxius* ♂. The antennal fluttering observed during courtship seems to be the same as that occurring during copulation. Compare the position of the antennae with the positions shown in figure 39.

ments(collectively, hereafter antennation) prior to probing with the aedeagus, and when insertion does not occur quickly, they are repeated during the probing phase. Antennation also occurs as the aedeagus is being inserted; it is repeated occasionally until the male starts the vibrant movements thought to attend insemination, and is performed following insemination as the aedeagus is being withdrawn.

No incontestable evidence could be found regarding the nature of the intersexual communication which leads to females accepting or rejecting males of a particular species. However, it does seem to have something to do with antennation by courting males.

If a female begins to move during insertion and the earlier phases of copulation, antennation appears to tranquilize her again. Exceptions occur in some interspecific pairings, or when females are unreceptive as a result of recent copulation. In these cases females usually run about despite antennation by males. Males may have difficulty withdrawing the internal sac and penis while the female is moving. This may be the reason for the occurrence of antennation as the aedeagus is withdrawn, and the selective advantage which favored the development of this behavior may stem from the reduction in incidence of injury to the male genitalia.

A comparison of the courtship behavior of *anxius*, *g. liragus*, and *horni* yielded some data concerning the basis for the unreceptivity of *horni* and *anxius* females to *g. liragus* males. During antennation the males of *horni* and *anxius* usually contact the head and pronotum of the female. *A. g. liragus* males, on the other hand, often do not touch the female with the antennae during courtship, and when they do, seem to do so very lightly. However, there seems to be too much intraspecific variation for this alone to account for the entire lack of receptivity of *horni* females for *g. liragus* males. Even when *horni* males seem to antennate very lightly, they are accepted by conspecific females, and the few times when *g. liragus* males appeared to antennate like *horni* males they still failed to elicit receptivity in *horni* females.

Examination of the scape and the antennal sockets of these insects at high

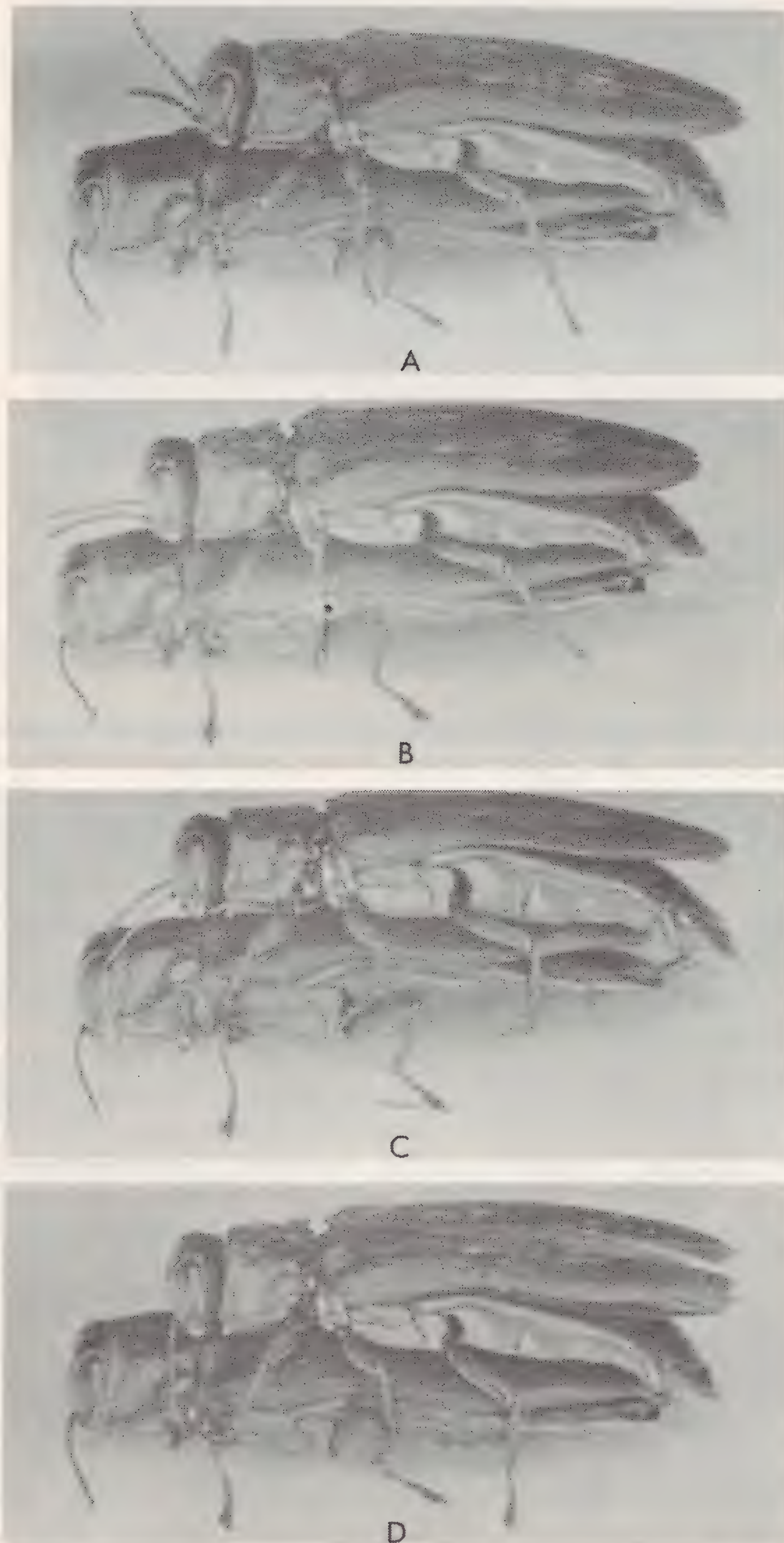


Fig. 39. Positions of the antennae during the stroking movements of males (here *Agrilus granulatus liragus*) in copulo or courtship, arranged sequentially: (A) being moved forward, (B) maximum anterior extension, (C) beginning of backward stroke, and (D) finish of backward stroke.

power (90X) indicates a remote possibility for high frequency vibrations or slight sounds being produced by some of the movements involved in antennation. The undersides of the scapes (reposed) are flattened and striate. Similar striations are found on the lateral rim of the antennal sockets and on the part of the front between the antennal sockets and the eyes (fig. 40). Movement of the scape over the striations on the antennal socket and front, as occurs during antennation, must produce some friction and thereby vibrations or sounds. The question is whether or not such vibrations or sounds could be intense enough to serve in communication. When the head is thrust forward during antennation (fig. 39, above), the increase in hydrostatic pressure should be transmitted to the antennae. This, in turn, may increase the friction between the scape and the striate surfaces on the antennal sockets and front.

The frontal striations are definitely strongest in horni, weakest in g. liragus, and of intermediate strength in anxius. Consequently, any sound or vibration produced might be somewhat species specific. In comparing the structures with other species in the anxius group, we found that some of them, vittaticollis for example, have even stronger frontal striations than horni. Perhaps these species should be studied first in an effort to determine the significance of the striations.

Stridulation

The possibility that other auditory, vibrational, or chemo-tactic communications might be responsible for species discrimination by females cannot be discounted. Both sexes do produce stridulatory sounds that have been recorded. The method of stridulation is one apparently peculiar to Agrilus, and has been reported for A. solieri Castelnau & Gory and A. cinctus Olivier (neither sp. in anxius group) by Schaefer (1949). It involves a rapid rotation of the head in its prothoracic socket. Males of anxius, pensus, g. liragus, or horni have not been seen making these movements during courtship. Moreover, the

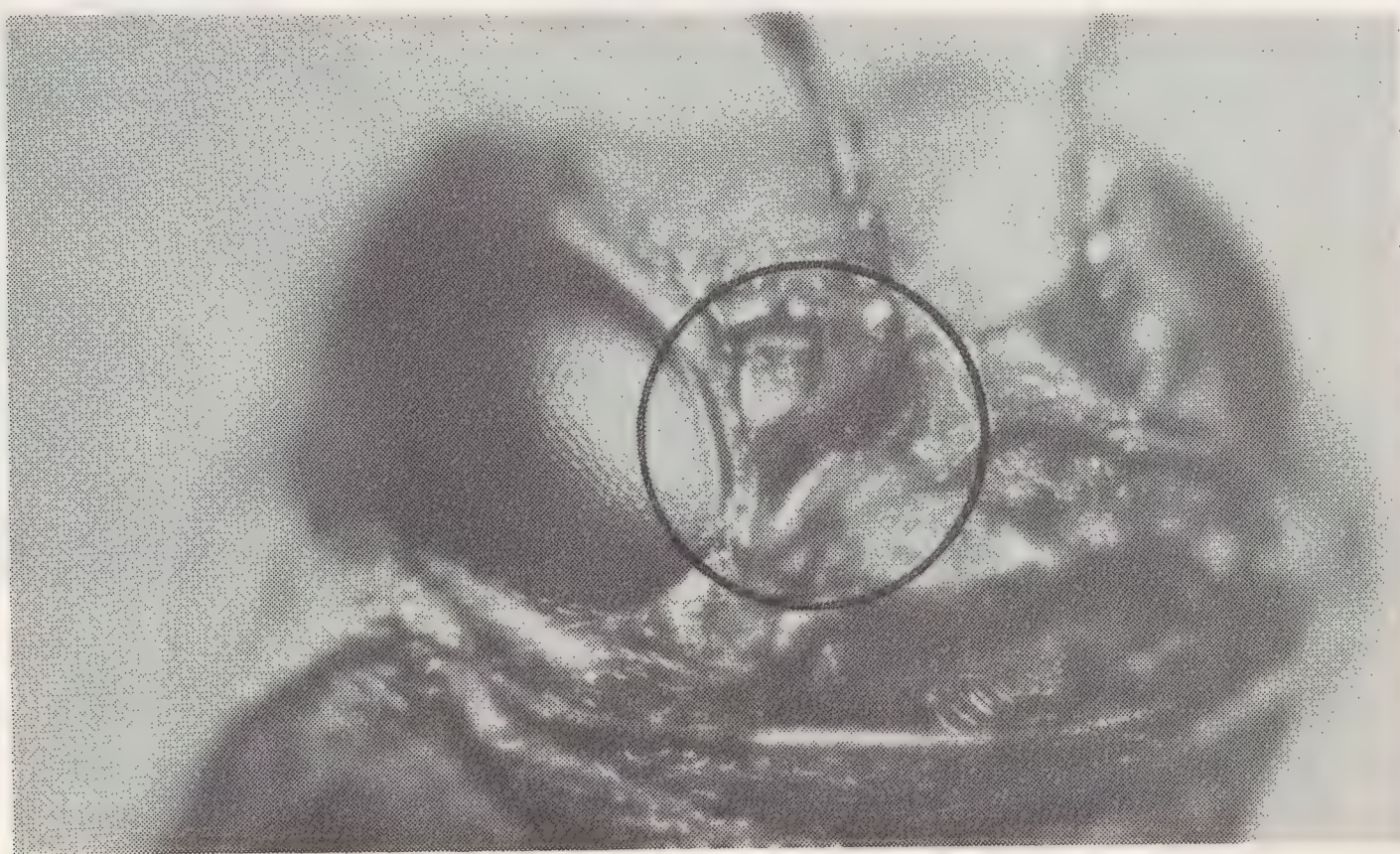


Fig. 40. Frontal view of Agrilus vittaticollis ♂ (X42); within the circle are the striate areas between the antennal socket and the eye and on the underside of the scape. The striations are coarser in this species than in horni, anxius, pensus, or g. liragus.

sounds produced by these stridulations seem to have no connection with female recognition of males in these species. The only time during courtship that the head is involved in pronounced movements is during antennation, after it has been thrust out of its prothoracic socket. The only situations in which stridulation has been noticed are ones which would indicate that the noises produced could be classified as stress sounds.

In stridulating these beetles tilt the head slightly forward at the top. This apparently brings the genal ridges¹ (the carinae at the lower edges of the genae; fig. 41) into position to contact the prosternal lobe. The genal ridges act as the scrapers, while the fine imbrications on the prosternal lobe serve as the file (fig. 42). The latitude of the rotational movements of the head during stridulation is quite small, in the neighborhood of a millimeter. Because of their rapidity it was difficult to count the movements, but there are approximately 5 head movements per second to each side of the center position. This agrees roughly with audiospectrographs (fig. 43) which show that the file is contacted about 10 times per second. The sounds produced are very soft. Consequently, it was rather difficult to record them.

As one might expect of sounds that are really only stress-induced, there is no indication that these *Agrilus* sounds are species-specific. These beetles probably do not produce other kinds of sounds with this same stridulatory apparatus. As previously noted, stridulation has not been observed in a situation that would definitely indicate that it was not stress-induced. There were a few indications that it may elicit repulsion of individuals that contact stridulating beetles. Alexander, Moore, and Woodruff (1963) suggest that, inasmuch as the sounds of Coleoptera are usually too soft to function at long distances, they may function in several fashions among adults in close proximity. The stridu-

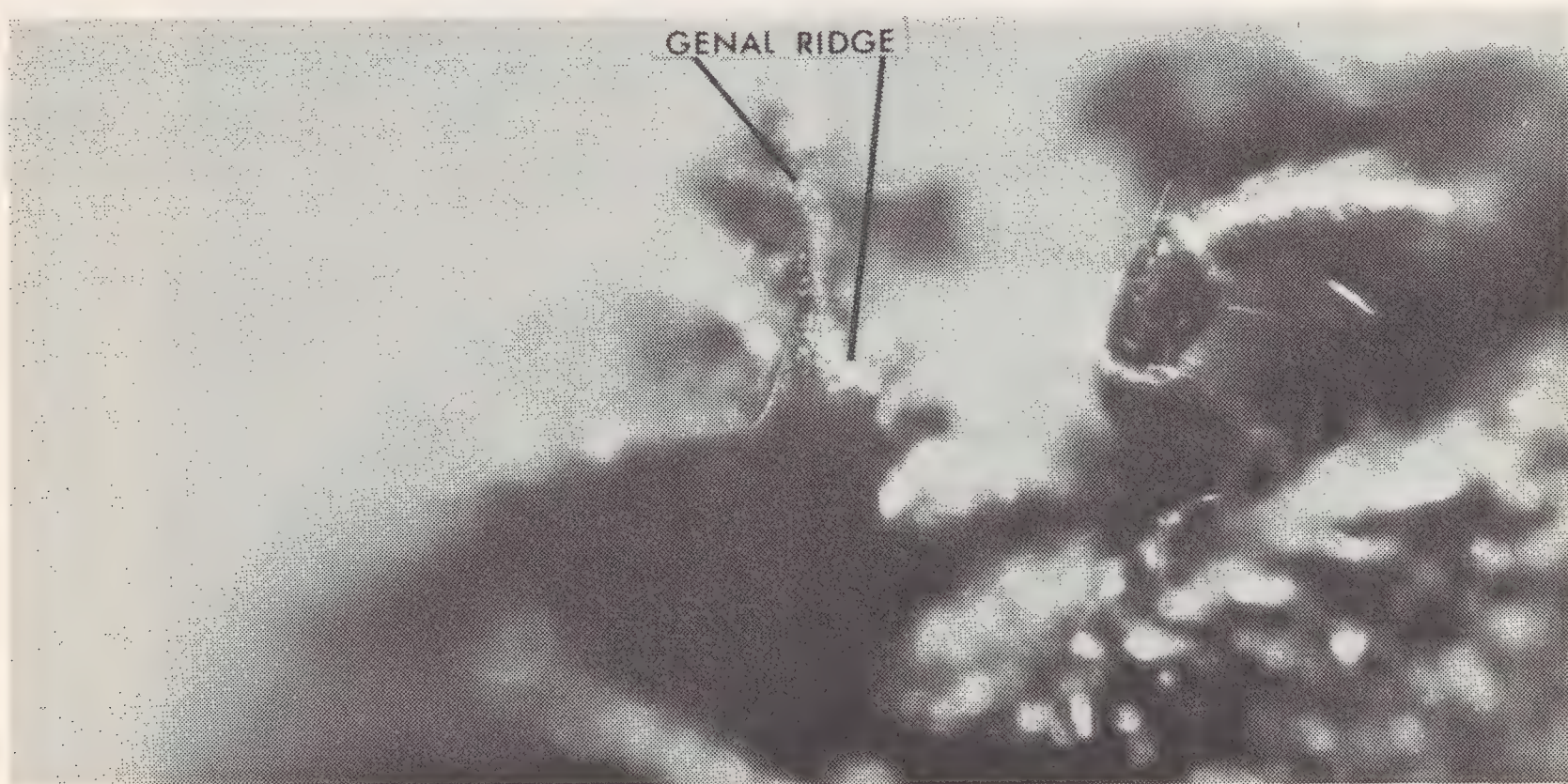


Fig. 41. Postero-ventral view of the head of an *Agrilus horni* ♀, showing the genal ridge (X109). Note the fine striations which are barely visible at one point near the posterior end of the ridge; they may be important in stridulation, but the sharp posterior portion of the ridge's outer edge may also contact the prosternal lobe (fig. 42).

¹Mr. G. B. Vogt, U. S. Dept. Agr., A.R.S., Entomology Research Division, Washington, D.C. believes that "genal ridge" is the best possible term for this structure (personal communication).

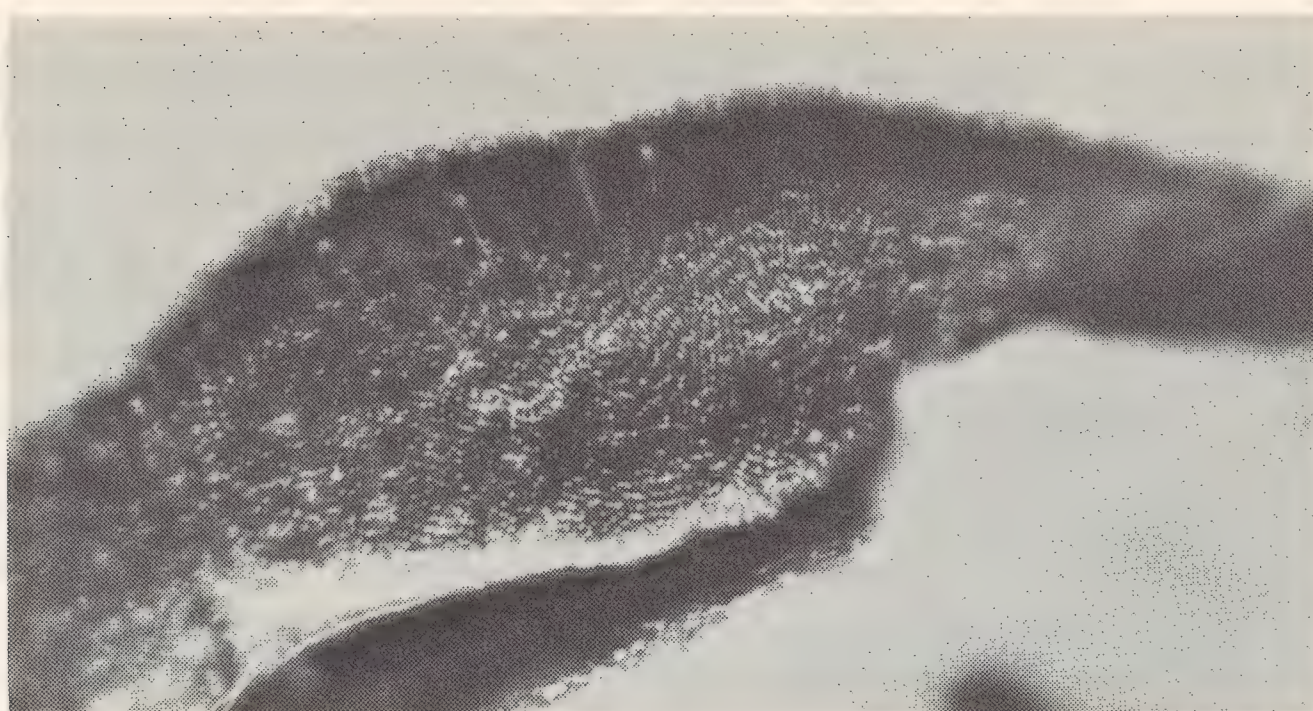


Fig. 42. Finely imbricate interior surface (head is excised) of the right half of the prosternal lobe of an Agrilus horni ♀ (X82).

latory apparatus of the species which were examined thoroughly (anxius, g. liragus, pensus, and horni) was not sexually dimorphic, and recordings indicate that there is no sexual difference in the sounds produced. They do not appear to be directly associated with courtship. Although unreceptive females may occasionally stridulate, their stridulation does not seem to have any effect upon courting males. In homosexual encounters, a sexually aggressive male is usually repulsed only after he mounts and probes the other, and stridulation does not seem to be involved. Nevertheless, stridulation may function in some other situations to prevent over-congregation of males or females, or they may serve to repel individuals of unrelated Agrilus species which may live on the same host. These stridulations should evolve toward nonspecificity in the eliciting stimulus (Alexander, et al., 1963). It is, therefore, difficult, if not downright impossible, to assess their significance by studying them under artificial conditions. On the other hand, as these Agrilus stridulations cannot be heard, except through amplification or by placing the insects next to the ear, and because the movements cannot be seen at distances of more than a foot or so, anyone endeavoring to determine their real function under natural conditions, will, to say the least, be faced with a real challenge.

EVOLUTION

Phylogeny

When our work on Agrilus was initiated, we had not pondered seriously enough the possibility that anxius, pensus, horni, and g. liragus are not all closely related. It seemed that the important questions to be answered concerned isolating mechanisms and clues to how these species evolved from a hypothesized common ancestor. Because of this improper assessment, more species than originally anticipated will be brought into discussions about phylogeny.

THEORETIC BASES . It is quite usual to regard some characters as more reliable than others as indicators of phyletic relationships. Nevertheless, we

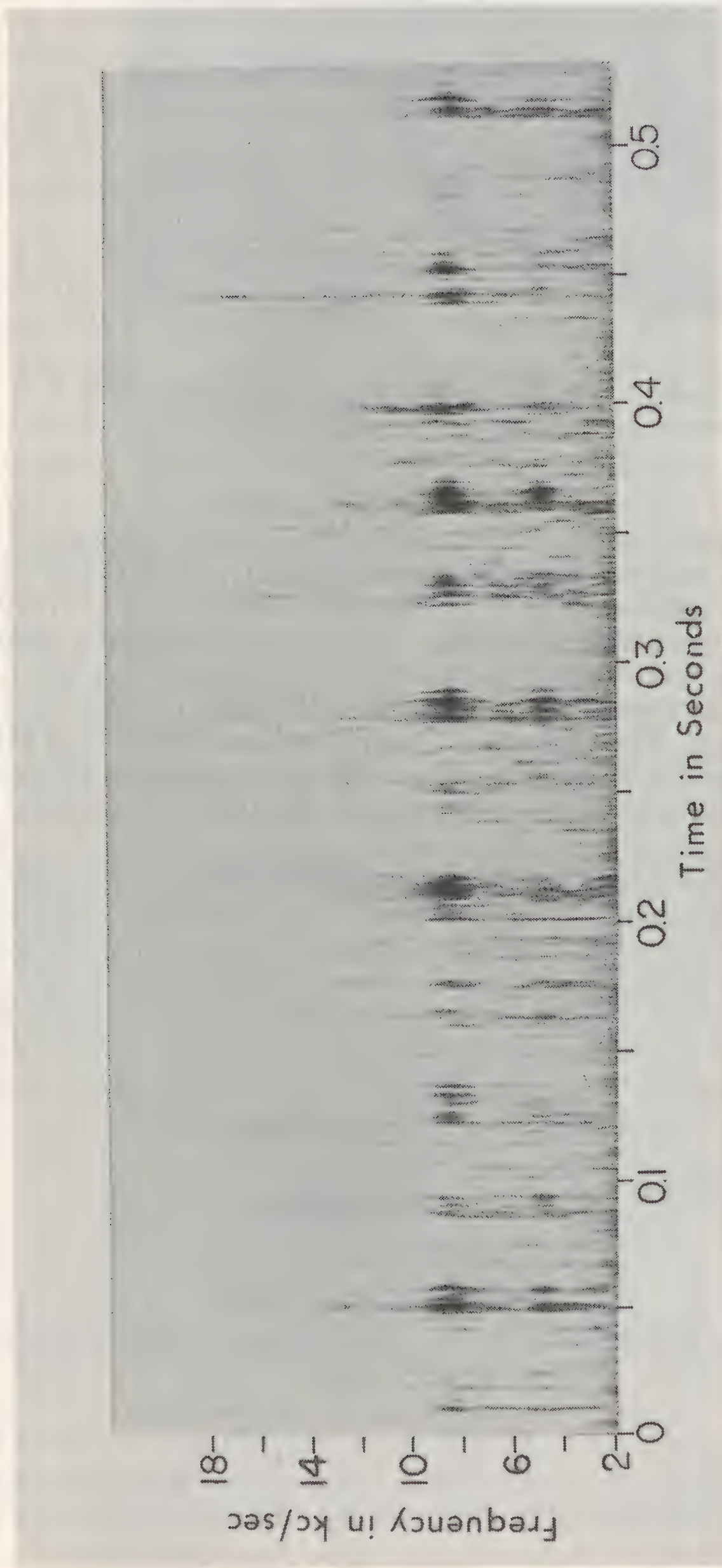


Fig. 43. Audiospectrograph of stridulatory sounds of an *Agrilus granulatus liragus* ♂. The tape recording was made with a Magnecord Model PT63A2HZ recorder, a Magnecord Model PT63-J amplifier, and an American Model D33-A microphone, at a tape speed of 15 inches per second. Two persons were required for making recordings. One held the beetles near the microphone and gave signals to the other, who operated the recorder. This allowed the microphone to be placed at a distance from the recorder, minimizing interference from sounds associated with operation of the recorder. The audiospectrograph was made with a Kay Electric Company Vibrilyzer, with signals fed in by the amplifier mentioned above, at 1/4 the tape speed of the original recording. Two runs were used to make the markings as dark as possible. The vibrilyzer settings were: mark level gain 8.0, wide band width, shape flat, high gear, and low motor speed.

shall set forth the assumptions concerning those we use, and give our reasons for not considering others to have the value accorded them by other students.

Let it be made clear at the onset, that we do not regard any characters as being "nonadaptive." Many systematists have used the term nonadaptive in reference to stabilized characters, while referring to those subject to much variation as "adaptive." The irrationality of the idea of adaptivity and nonadaptive is discussed by Dobzhansky (1956), who maintains that all traits, or at least the vast majority of them, are adaptive or have been adaptive at some time in the history of their development. To be sure, some traits are more stable than others, but their stability should relate to the kinds of functions rather than to the existence of functions versus the lack of them.

In many cases it is difficult to perceive functions for some seemingly trivial traits, but this is a poor reason for assuming they do not exist. So it is with the pygidial spine of species in the Agrilus anxius group. Without searching for its function, one might take what seems to be the prevailing attitude in such cases--that its stability indicates that there is no selection against it, probably because it is of no great disadvantage to its possessor. Quite to the contrary, it seems that the stability of the pygidial spine stems from its importance in the process of sexual recognition. Any large changes in the form or size of the pygidial spine calls for corresponding changes in the form of the male aedeagus and other structures. In genetic terms, it probably owes its stability to an association with pleiotropic genes whose total influence on the developmental system is spared extensive changes through the moderating influences of homeostasis or coadaptation (see Dobzhansky, 1956).

The pygidial spine probably has at least as much stability as characters ordinarily given tribal or generic value in other insect groups. Perhaps Obenberger was the one taxonomist who should have had sufficient worldwide familiarity with Agrilus to recognize this, but he was convinced of the impossibility of even dividing Agrilus into acceptable subgenera (see Obenberger, 1959). What Obenberger (1957) implies is that, to be valid, each proposed subgenus must have as its basis a single character which occurs among no species of other groups. If any Agrilus character could meet this absurd requirement, it would probably be the pygidial spine. Obenberger (1957) denies this possibility because (1) a pygidial spine is found in the Palearctic forms Agrilus guerini Lacordaire, A. fleischeri Obenberger, and A. ater L., but is absent in an alleged intimate ally, A. suenisoni Obenberger; (2) its presence among about 30 African species makes it self-evident that it occurs among entirely unrelated groups.

To counter the first point one need only ask what criteria he uses to ally suenisoni with ater and the rest. He offers none, and almost any should be more subject to convergence than the pygidial spine is to total disappearance. Obenberger's second point is even more indefensible because the presence of the spine among African species cannot, in itself, demonstrate that it has arisen repeatedly. There is no á priori reason for believing that even the Ethiopian species he mentions do not share common ancestry with Palearctic ones. After all, the Palearctic region does extend into northern Africa.

INTERPRETATION. Fisher (1928) has given the form of the tarsal claws precedence over the pygidial spine in his classification. As a result, three species which are here placed in the anxius group are classified quite apart from it by Fisher. These are Agrilus ruficollis, A. champlaini Frost, and A. browni (= lateralis, sensu Fisher [1928]; see p. 6). The bifid claws of these species

have the inner lobes bent toward each other. This trait appears to be the only one which they have in common with the species Fisher places them near. The pygidial spine, the marginal sclerite of the hind segment, and the general form of these insects links them with species in the anxius group.

On the other hand, ruficollis, browni, and champlaini have more in common than just similar tarsal claws. They resemble each other in the structure of the pronotum, elytra, and male or female genitalia. In addition, ruficollis and browni are similar in coloration. Their hosts are not closely related, but the larval habits of all three species are somewhat alike. The larvae of ruficollis bore in the stems of brambles (Rubus spp.). During the early stages of development they often (cf Smith, 1892) form galls by making a tight spiral in the phloem, while late-instar larvae move rather directly up and down the pith. A. champlaini forms galls on ironwood (Ostrya virginia) and blue beech (Carpinus caroliniana), but the late-instar larvae spiral mostly in the wood within the gall which forms as the result of the phloem blockage caused by the gallery of the early instars. Fisher (1922) reared browni from bayberry (Myrica pensylvanica), and Knull (1922, 1950) says Myrica asplenifolia is also a host. The browni larvae make no galls. According to Fisher (1922), after passing the winter in the roots, the browni larvae spiral upward in the limbs for a considerable distance before they reach maturity.

The number and variety of similarities between ruficollis, browni, and champlaini makes it unlikely that they could all be convergent. However, these species differ in ways that seem to push their divergence to a rather remote era. For example, it does not seem likely that a species living on Ostrya and Carpinus could be intimately allied with species whose hosts are Rubus spp. or Myrica spp. Consequently, in figure 44, champlaini is shown as also having remote connections with species that live on Fagaceae, which includes Agrilus bilineatus, A. acutipennis Mannerheim, and a number of other forms. While champlaini might instead be related to the line represented by anxius and its allies, it appears to resemble bilineatus and related species in a greater number of minor respects. For instance, the latter have the inner lobes of the tarsal claws turned inward, although to a lesser extent than does champlaini.

Allies of horni. A. browni seems to be more closely related to horni than to ruficollis (fig. 44). While its tarsal claws are like those of ruficollis, browni resembles horni in having the vertex less strongly impressed, the front flattened, and the marginal sclerites of the abdomen clothed with white pubescence. The browni aedeagus is intermediate in form to those of ruficollis and horni, but browni has a trace of the prehumeral carinae, which are completely lacking in ruficollis.

While the eggs of ruficollis are placed at the axils of the branches (Hutchings, 1922b) or leaves (Smith, 1891) of its hosts, those of browni and horni are placed at the bases of the host plants. The larval habits of browni and horni are very similar (excluding host differences). In each case the larvae bore into the roots and over-winter there. The only difference is that horni bores farther out into the root and spirals back to the stem, while browni spirals mostly in the branches. The early-instar ruficollis larvae, on the other hand, over-winter in the stem and probably spiral only during the time prior to this initial overwintering period.

Agrilus vittaticollis has the vertex strongly impressed as in ruficollis. Fisher (1928) says vittaticollis is allied with benjamini Fisher and audax Horn. The host of benjamini is unknown, but audax infests the upper branches of Ulmus

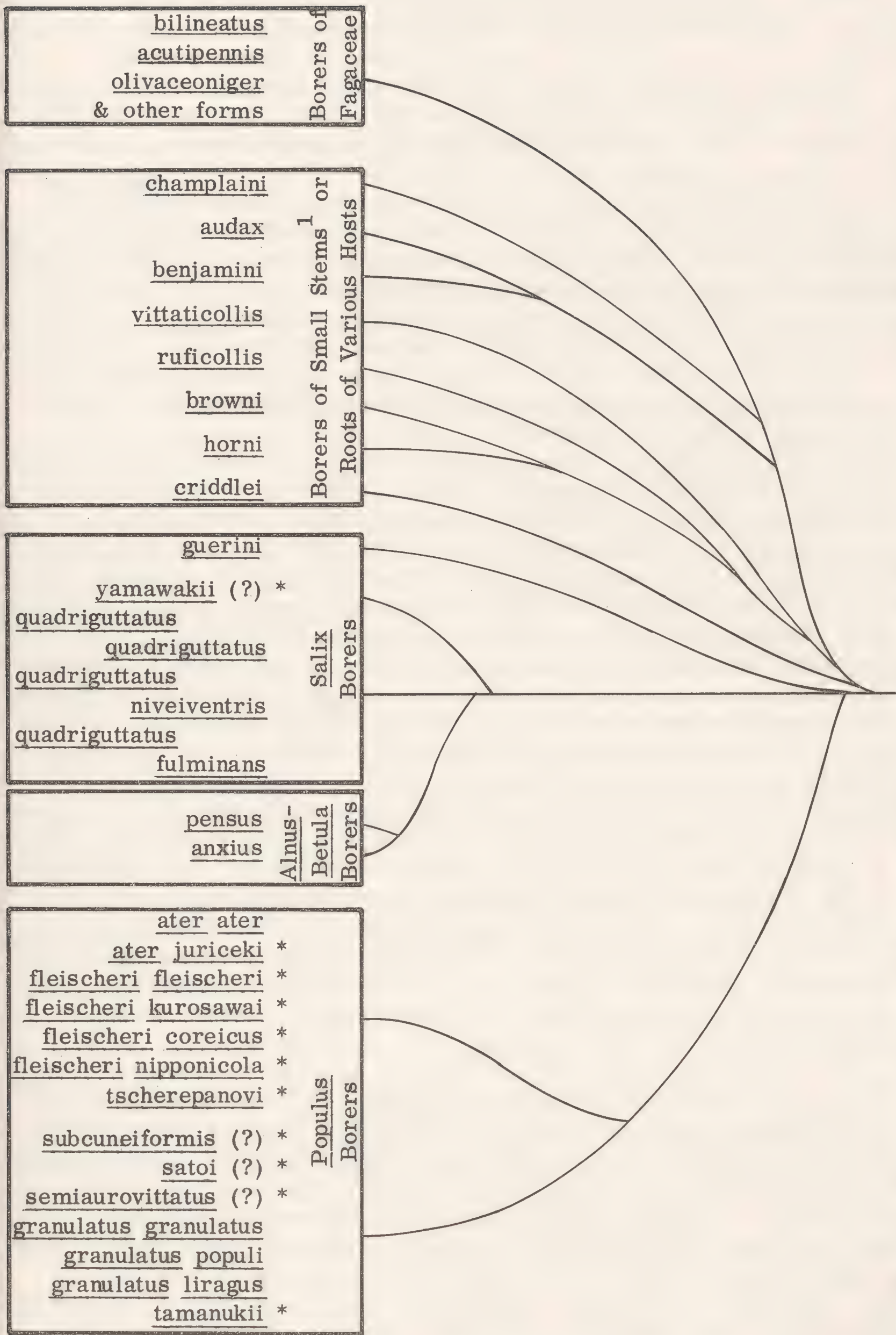


Fig. 44. Hypothetical phyletic tree for some of the described Nearctic and Palearctic forms placed in the Agrilus anxius group. The names of taxa of which the authors have seen no specimens are marked with an asterisk. A question mark follows the names of those species for which the designated host specificity is uncertain.

¹Also includes gall-making species.

rubra (Knull, 1934). A. vittaticollis, however, has a root boring habit quite like that of horni, but in its morphology vittaticollis bears more similarity to ruficollis. Hence, vittaticollis is shown (fig. 44) as sharing common ancestry with ruficollis, browni, and horni, but splitting from them before they diverged from each other.

Without exception, horni has always been classified as a close ally of anxius, on the basis of coloration, the structure of the claws, and the form of the prehumeral carinae. The superficial resemblance of these species is, in fact, so close that without a knowledge of their biology this alliance would seem most probable. It is almost axiomatic that coloration is an unreliable indicator of phyletic relationships. The amount of variation which the prehumeral carinae show throughout the genus, and indeed their complete absence in numerous species, even within the anxius group, suggests that they are also unreliable and should be used for classification only with particular caution. The morphology of the tarsal claws appears to be of a similar nature. Nothing more than wild speculations could be offered for explaining why these characters should be variable among species, but relatively constant within. Nevertheless, there probably are sound and logical reasons for it being so.

Probably the most significant morphological features which appear to link horni with browni, rather than anxius, are found in the structure of the male and female genitalia. In browni and horni, the ovipositor is half as long as that of anxius (relative to total body size). In correspondence with the female genitalia, the aedeagus in browni and horni is shorter than that of anxius.

There are a number of other minor characters which seem to separate horni from anxius, g. liragus, or pensus and show its relationship to browni. (1) In horni and browni the marginal sclerites of all abdominal segments, except the last, tend to be rather densely pubescent, but in anxius, g. liragus, or pensus the second marginal sclerite tends to be glabrous. (2) The striations on the antennal scape and on the front, between the antennal socket and eye, are nearly as strong in horni as in browni, while they are weaker in anxius and, particularly, g. liragus. (3) The elytra of horni and browni tend to be evenly sculptured and rather evenly clothed with pubescence that is uniformly short. Those of anxius, g. liragus, and pensus are not sculptured as evenly, having a longitudinal costa and a depression mesad of the costa and between the basal third and apical half of the disc. Frequently in g. liragus, and less often in anxius and pensus, this depression is pruinose. The hairs on the elytra of the latter three species are not uniform in length, nor are they evenly distributed. They are sometimes very closely spaced near the suture, about halfway between the midpoint and apices, particularly in pensus.

A. horni also resembles browni in a number of non-adult characters, that are different in anxius and its allies. According to Fisher (1922), the eggs of browni turn black before hatching as do those of horni. Those of vittaticollis darken in the same manner (Brooks, 1913). The eggs of anxius and g. liragus turn yellow or light brown prior to hatching. Barter (1957) says that anxius eggs are covered with a whitish liquid by the female after a group of them has been laid. None of the various workers who have observed horni, browni, and vittaticollis have mentioned that such a substance was applied to the eggs of those species. However, according to Mundinger (1941), ruficollis sometimes covers its eggs with such a substance, but often leaves them nearly naked of the covering.

After the first instar larvae of horni, browni, and vittaticollis bore out of the egg, they go directly to the roots of their hosts. It appears that the lar-

vae of these species over-winter in the first instar, and generally bore much farther than anxius or g. liragus before undergoing the first molt. The latter species usually molt to the second instar soon after they enter the phloem, and their pupal chamber is often formed during the same year that the eggs are laid. Even when first instar horni larvae were introduced into aspen logs, they bored for long distances without molting before succumbing¹. Apparently, for the larvae of horni, browni, and vittaticollis, the first molt is elicited by a very different set of conditions than are necessary for its occurrence in anxius or g. liragus.

Theoretically, at least, the most significant way horni differs from anxius or g. liragus is in its mode of host selection. A. anxius and g. liragus live on decrepit hosts, and seem to be attracted to them by odors given off as a consequence of the biochemical deterioration associated with decrepitude. On the other hand, horni seems to depend upon thigmotactic means for distinguishing poplar suckers of suitable sizes from unsuitable ones which are apparently no more or less vigorous.

Hybrid crosses between anxius, g. liragus, and horni were made, but do not seem to substantiate other evidence concerning their phyletic relationships. The following crosses yielded viable eggs: ♂ horni X anxius ♀, and the reciprocal; ♂ horni X g. liragus ♀²; and ♂ g. liragus X anxius ♀ (no reciprocal eggs).

First instar larvae of all crosses yielding viable eggs were introduced into aspen and birch logs. Some larvae of all hybrids developed at least partially. However, late-instar galleries were formed by ♂ anxius X g. liragus ♀, and one ♂ horni X g. liragus ♀ imago emerged. This one hybrid beetle, a female, has characteristics of both parental species. The ovipositor is of the normal length for g. liragus, and the elytra bear a pair of faint efflorescent spots. On the other hand, the marginal sclerites of the abdomen are uniformly pubescent and the pronotum has a distinct cupreous tinge, which are horni traits. This hybrid was fully receptive to horni males, but unreceptive to g. liragus males. The only abnormality noticed was a possible deformity in the articulation of the tarsal claws. However, it is not absolutely certain that their condition is really abnormal because the claws were not examined before the hybrid died and had dried out.

If the conclusions regarding the phyletic positions of horni and g. liragus had been drawn before the hybridization tests were performed, inviability of the eggs would have been expected. The successful rearing of a ♂ horni X g. liragus ♀ adult is a rather baffling perplexity. However, the success of this cross seems no more phenomenal in view of its wideness per se than it is in light of the known differences in the chromosome numbers of horni and g. liragus.

It is possible that A. olivaceoniger Fisher is related to browni and horni. Although olivaceoniger lacks prehumeral carinae, browni has only a trace of them. The form of the olivaceoniger tarsal claws is intermediate between the browni and horni forms. In most other features, all three are very similar. Nothing certain is known of the biology of olivaceoniger. Blanchard (1889), calling it the olivaceous variety of acutipennis, said it occurred on poplar sprouts in

¹ The work of Engel (1968) seems to indicate that the behavior of horni larvae can be similar to that of the larvae of g. liragus or anxius, depending upon host condition.

² The reciprocal of this cross could not be assessed because no horni females were receptive to g. liragus males.

Massachusetts. Frost (1912), on the other hand, claimed to have encountered it quite often on oak, which would indicate that it may really be related to acutipennis.

Fisher (1928) places olivaceoniger near criddlei and acutipennis. While acutipennis appears to be related to bilineatus and allies (fig. 44) and lives on Quercus spp., criddlei lives on willows and is related to the Salix borer group. However, criddlei is not placed in the latter group because it has traits which also indicate a relationship to horni and its allies.

Because criddlei is a gall-former, its mode of host selection may be similar to that of horni. The habits of the larvae are more like those of horni than those of species in the Salix borer group. During the earlier stages of development, the criddlei larvae spiral in the phloem, but they later feed mostly within the xylem (cf Wong and McCleod, 1965).

A. criddlei resembles horni in having a deep, smooth median groove on the first and second abdominal sternites of males. Of the forms in the Salix borer group, quadriguttatus quadriguttatus has the strongest abdominal groove, but it is not as well-developed as in criddlei. This groove is weakly developed in males of q. niveiventris and q. fulminans, but absent in A. guerini Lacordaire, a Eurasian species (see Stepanov, 1954).

The male and female genitalia of criddlei are very similar to those of horni, although the apex of the criddlei penis is acuminate (fig. 45) instead of rounded as in horni. The penis apex of quadriguttatus and subspecies is acuminate like that of criddlei. The elytra of criddlei and those of species in the Salix borer group are also very similar. In addition to having the tendency for the formation of discal spots of pubescence, the elytra of all of these species are angulate at the apex (fig. 46a, b). This latter feature of the elytra appears to have reached its maximum development in guerini, which has greatly prolonged elytral apices with a very deep notch between them (fig. 46b).

The Nearctic Salix borers have well-developed prehumeral carinae. These carinae are not strongly developed in criddlei and are only rudimentary in guerini. The evidence suggests that criddlei may be a rather direct descendent of the form ancestral to the triad of groups composed of the Salix borers, Populus borers, and Alnus-Betula borers.

The Salix Borers. Of this latter triad, the Salix borers seem to be the least specialized. According to several accounts of its larval habits, guerini usually bores in the upper branches of willows (Gaudin, 1921, Lecomte, 1925; Horion, 1955; Lundberg, 1962), and its larval habits are quite analogous to those of pensus. The larval habits of the other species of Salix borers are essentially unknown. The size of the willows which serve as hosts of q. niveiventris and q. fulminans (e.g. Salix lasiandra and S. lasiolepis) suggests that these Agrilus may have larval habits quite similar to those of guerini. It does not seem likely that the larval habits of nominal quadriguttatus would differ markedly from those of its other subspecies, but the former has as its host the black willow (S. nigra)¹, a very large tree at maturity. Therefore, q. quadriguttatus could have habits analogous to those of anxius or g. liragus.

Agrilus yamawakii Kurosawa is a Japanese species (Honshu, Shikoku, Kyushu), which shows some resemblance to the Nearctic Salix borers. The figure in Kurosawa (1957) shows a rather unusual undulate band subapically on the ely-

¹In reference to q. quadriguttatus Fisher (1928) said: "This is probably the species recorded as having been collected on partly dead alders (Alnus sp.), although no specimens have been examined which were collected on that plant." This is an obvious reference to the statement of Blanchard (1889) regarding the series from which Horn (1891) described pensus (granulatus, sensu Blanchard [1889]).

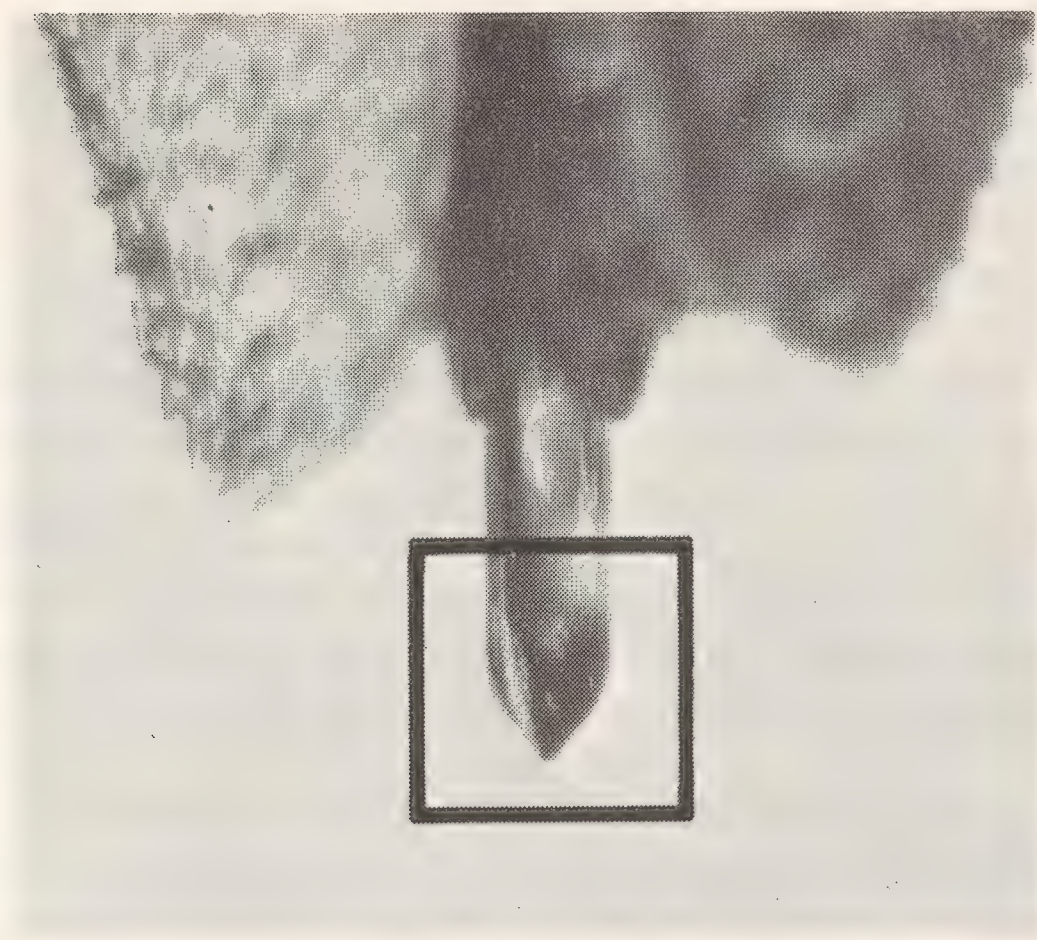


Fig. 45. Penis apex of Agrilus criddlei.

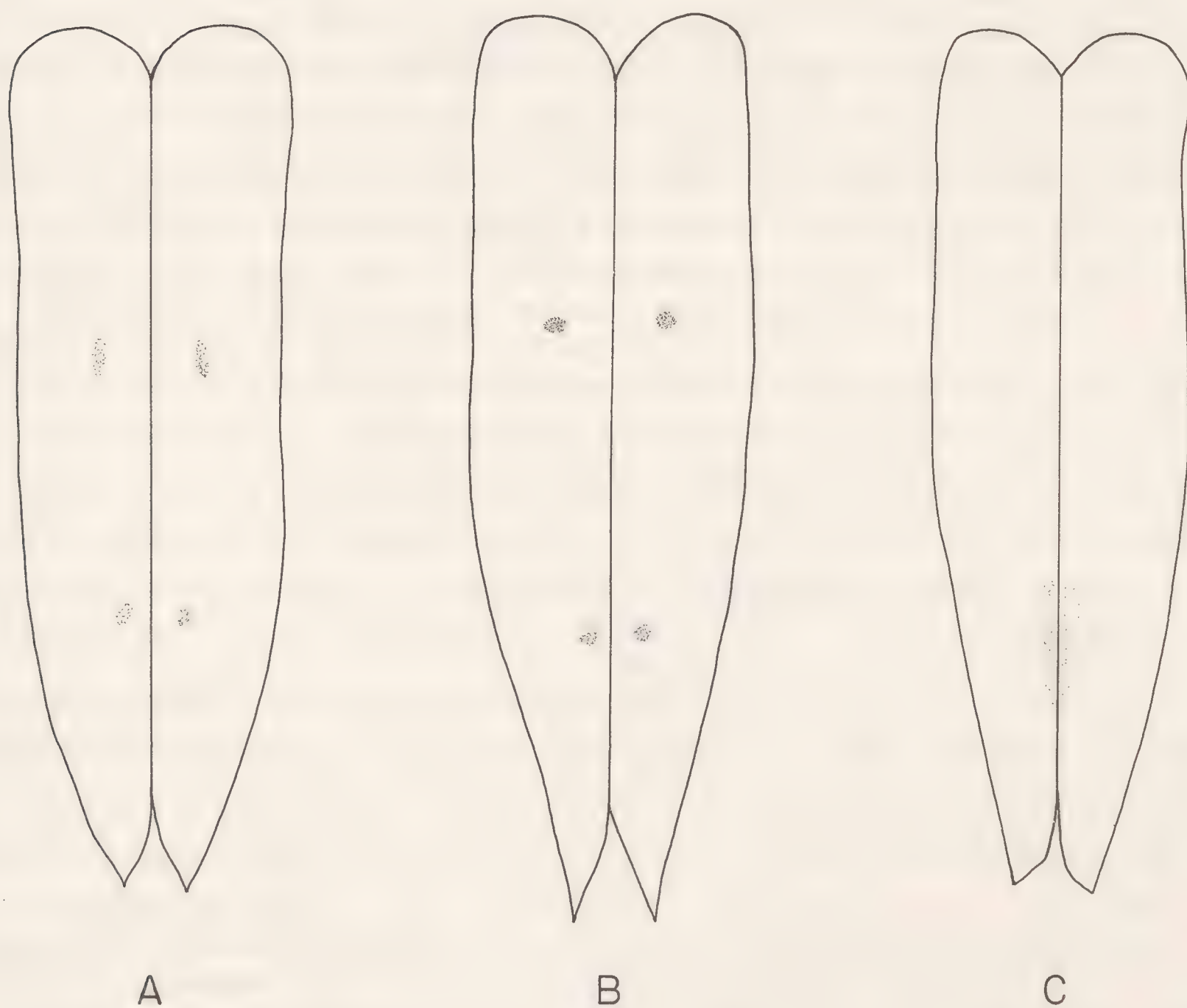


Fig. 46. Elytra of Agrilus ater (A), A. guerini (B), and A. quadriguttatus niveiventris (C). Figures of ater and guerini redrawn from Théry (1942).

tra of yamawakii, and there is no mention in its description of a median basal groove on the abdomen of males. However, its habitus is otherwise so much like that of quadriguttatus and subspecies that it is included as a possible member of the Salix borer group.

Agrilus guerini is the only Palearctic species in the anxius group that has been reared from willows. On the basis of its discontinuous east-west distribution in Europe, Horion (1950, 1955) considers it to be a postglacial relict of a tropical group. Théry (1942) comes to similar conclusions because of the peculiar form of the elytra. To be sure, there are a number of tropical forms with elytra similar to those of guerini (see Obenberger, 1957), but they do not appear to be at all related to guerini as they lack the pygidial spine. The type of A. nevadensis Horn, which is a synonym of q. niveiventris Horn, has elytra prolonged somewhat like guerini, but those of guerini are longer and more arcuate on the inner margin.

The Alnus-Betula Borers. The Populus borers and the Alnus-Betula borers probably arose independently from a Salix boring ancestor. Moreover, it is highly unlikely that the switch from willows to a host in the birch family could have been made by a specialized form similar in habits to anxius or g. liragus. There would, in theory, have been obstacles to its occurrence in this way. Host selection of anxius and g. liragus seems to be strongly reliant upon airborne by-products of biochemical degradation from hosts that are injured or under severe physiological stress. Although an attempt will be made later to discredit the assumption that anxius and g. liragus are closely allied and that there are no intermediate species, let it be assumed for now that the assumption is valid. In addition, let it be assumed that anxius was derived from a Populus borer, although the direction of the change is immaterial to the development of the theoretical case¹. The foregoing assumptions yield three anomalies. (1) The Populus borer ancestral to anxius would have to be preadapted for detecting those chemical substances of birches that would indicate the equivalent of the conditions it was adapted for on Populus. (2) Implicit in the definition of pre-adaptation is the necessity that the foregoing occurred in the absence of Betula spp., but the latter presently occur in most of the areas where Populus spp. are found. (3) The alternative to a hypothesis of preadaptation is for the capacity to recognize equivalent conditions in Betula to have developed gradually in the Populus borer. Those accepting this hypothesis are left with the problem of explaining a sudden discontinuity (sympatric speciation) in the flow of genes between the Populus borer and the newly-developing population of the Betula-boring form. Explaining the irreversibility of the Populus-to-Betula transition is also problematical.

It is much more logical to theorize that the switch was made by a form much less specific to host conditions, and more specific to certain parts of a host (e.g. certain sizes of limbs, or limbs versus trunk, etc.). Chemo-sensory recognition of the host is not as crucial a matter in this case, allowing a little more opportunity for evolutionary trial and error. Besides one has a possible transitional form, or a fairly direct descendent of it, in Agrilus pensus.

Barter and Brown (1949) have suggested the pensus is allied with g. populi Fisher, but their resemblance is merely superficial. The similarity of the coloration in these two forms may reflect, in part, adaptation to somewhat similar climatic conditions for their adult life spans, even though they occur on opposite sides of the continent. The pensus aedeagus is unlike that of g.

¹Smith (1949a) suggested the reverse (i.e. that g. liragus was derived from anxius).

populi or g. liragus, contrary to Barter and Brown (1949). Although few g. populi males with the genitalia extruded were seen, we have examined the genitalia of many g. liragus males. The aedeagus of pensus is actually more like that of anxius than that of g. liragus (see figs. 5 & 8, above).

Agrilus pensus is related to anxius and has some subtle traits which also link it with the Salix borers. The head is often flattened or broadly impressed on the vertex as in q. niveiventris and the apices of the elytra often resemble those of the Salix borers. About halfway between the midpoint and apices of the elytra and near the suture, quadriguttatus and its subspecies often have an elongated maculation formed by closely spaced pubescence (fig. 46c, above). A similar maculation occurs in pensus (fig. 4c, above). The ecological similarities of alders and willows also render strong support to the hypothesis that the transition from the Salicaceae to the Betulaceae was achieved by a species from which pensus has descended rather directly. Figure 44 shows a Salix boring species engendering an Alnus-Betula borer later than the evolution of a Populus borer from a Salix borer. We postulate this because there are no records suggesting that the Alnus-Betula borers are not endemic to the Nearctic region.

The Populus Borers. There are, on the other hand, a number of Eurasian forms in the Populus borer group. One of them, A. ater L., may be more closely allied to the Salix borers than any of the other Populus-boring forms. Nevertheless, the listing of willow as a host for ater by Horion (1955) and other taxonomists has dubious reliability. We have never seen a reference which either cites a particular worker as having reared ater from willow or gives other rearing records. One must be skeptical of these unverified records for ater, because they may very well be referable to guerini instead. The biology of ater is discussed by Krogerus (1922) and Kangas (1942a, b); it appears to have habits roughly analogous to those of Nearctic Populus borers.

A. ater males do not have a median groove on the basal abdominal sternites. In this respect ater appears to resemble guerini. In species which have an abdominal groove, it appears to function in properly aligning males during the act of probing and insertion of the aedeagus. In ater and guerini, the development of very sharply pointed elytral apices the enlargement of the notch between them, may have functionally supplanted the abdominal groove of males. The pointed elytra and absence of an abdominal groove in both species could indicate a rather ancient relationship and a rather direct descent from the pair of allied species proposed as the primordial Populus and Salix borers. However, the elytra of ater are shaped much like those of other Populus borers, while those of guerini appear to be an elaboration of the usual Salix borer type. Therefore, the extreme acuteness of the elytral tips and the associated loss of the male abdominal groove may be convergent developments in these two species. It is unlikely that the shape of the elytral apices bears any functional relationship to physical characteristics of the host. Hence, the consistent difference in the elytra of Salix and Populus borers should accurately reflect phyletic relationships.

Stepanov (1954) names poplars as hosts for A. fleischeri Obenberger, A. ater juriceki Obenberger, and A. tamanukii Stepanov. He says that A. tscherepanovi Stepanov lives on Populus laurifolia, which is grouped with the balsam poplars. If A. fleischeri coreicus Kurosawa, A. fleischeri nipponicola Kurosawa, and A. fleischeri kurosawai Obenberger have been properly classified as subspecies of fleischeri, they are also Populus borers.

A. tamanukii probably relates more closely to Nearctic Populus borers

than other Eurasian forms. Like the Nearctic forms it has a median groove on the basal abdominal sternites of males¹. It was described from southern Sakhalin, which, according to Tatewaki (1963), has a mixture of temperate east Asiatic and subarctic phytogeographic elements. Therefore, this species is an ecological counterpart of the Nearctic g. liragus and it is entirely possible that tamanukii should also be ranked as a subspecies of granulatus.

Three Taiwanese species, which also have a male abdominal groove, are put in the Populus borer group only on the basis of their descriptions. They are A. subcuneiformis Kurosawa, A. satoi Kurosawa, and A. semiaurovittatus Kurosawa. These species could be ecologic analogs or homologs of g. granulatus and g. populi.

Obenberger (1958) believed that more aberration and subspeciation has occurred among Palearctic buprestids than in those of the Nearctic region. Nevertheless, it seems unlikely that the number of Eurasian species and subspecies of Populus borers could be as great as the number of available names. The number of names needed for them will probably be reduced by synonymy in the future.

Zoogeography

ASSUMPTIONS

Effect of Climatic Change. The climates to which each of these Agrilus taxa are now adapted are probably similar to those in which they diverged from their closest allies. Climatic change undoubtedly led to much of the geographic fragmentation precursory to their speciation and subspeciation. The necessity of geographic isolation for speciation is generally acknowledged; models for sympatric speciation, except in a few special cases, appear unsupportable (Mayr, 1963).

Deevey (1949) says "the occurrence of closely related species in the same area implies their differentiation in previous isolation; this isolation must have lasted long enough, first to produce the reproductive divergence necessary to avoid swamping of one by the other, and second to produce the ecologic differentiation (differences in food habits, temperature preferenda, etc.) necessary to avoid too stringent competition. Nearly all well studied cases of subspeciation and speciation point to the Pleistocene as the time of previous isolation, and the occurrence of closely related forms in the same area is therefore attributed to post-Pleistocene alterations in geography and in biogeography."

One must certainly expect exceptions to such a sweeping generalization as this. However, the pitfalls to be encountered in its application are fewer than are met with in trying to decide which pairs of species are really siblings and which are not. Indeed, the important factors contributing to recent speciation and subspeciation among Nearctic forms in the Agrilus anxius group seem to have been the changing positions of glaciers, deserts, and prairies in relation to forested areas and mountain ranges.

Pigmentation. Coloration, for the Agrilus in question, appears to be mostly a matter of climatic adaptation as opposed to being cryptic. The results of studies among other groups of insects have interesting parallels which are

¹Neither Stepanov (1954) nor Kurosawa (1954) seem to have recognized this as a male character, and may, consequently, have described males and females of the same species under different names.

probably meaningful. Dobzhansky (1933) found that in certain Coccinellidae there is a marked concentration of scarcely pigmented varieties in Turkestan, Iran, California, and Mexico. The further a region is removed from these centers, the darker is the average type of population found therein. The darkest forms were found in eastern Siberia. Dobzhansky acknowledges a general agreement of his findings with Allen's rule, which according to him is more properly called Gloger's rule. This rule relates depigmentation of animals to arid regions, and pigment accumulation to humid regions.

Netolitzky (1931) derived similar kinds of rules from studies of Carabidae. He relates variations in pigmentation more to differences in altitude and latitude than to humidity. According to his findings, pigmentation of European carabid beetles increases with increasing altitude and latitude.

Kalmus (1941) gives some working hypotheses (he calls them laws) regarding pigmentation that are more elaborate and combine some of the features of Gloger's rule with those of Netolitzky's rules. He starts from a set of theoretical premises which are based upon the structure of insect cuticle and the attributes associated with the nature of its pigmentation. Kalmus says, "darkening and hardening of the cuticle are one in the same process." Whether or not this is entirely true is still a controversial matter (Cottrell, 1964). Kalmus (1941) attributes several different functions to hardening and darkening. He maintains that the functional attributes of the cuticle which are enhanced with increasing hardening and darkening are (1) heat absorption, (2) protection from high frequency radiations (i. e. ultraviolet), and (3) moisture retention.

There seems to be no logical reason for contesting the validity of the assumption that dark cuticles are more heat-absorbent than pale ones, and it is supported, in a small way, by the experiments of Buxton (1924). Kalmus (1941) generalizes that if the mode of life of an insect makes heat absorption advantageous, its coloration will be dark; if heat absorption is irrelevant or disadvantageous it may be pale. He also maintains that melanic forms are found at high altitudes because their dark cuticles give them greater protection from high frequency radiations. This may be true, but the effects of increasing high frequency radiation and those of decreasing temperature with increasing altitude cannot be mutually exclusive. His suggestion that insects exposed to drought are dark seems to be antithetic to Gloger's rule. Moreover, it might be contradictory to relate hardening and darkening to aridity were it not for the fact that iridescence is often associated with aridity. Many arid regions are also hot, but iridescence would seem to be compensatory; according to Kalmus (1941) it is associated with darkened cuticles, and gives them the heat absorbing qualities of pale coloration in combination with the moisture retaining capabilities accompanying heavy sclerotization.

Fisher (1928) was not cognizant of the close alliance between q. quadriguttatus and q. niveiventris, but thought that each of these Salix borers was related to its sympatric Populus-boring counterpart, g. granulatus and g. populi, respectively. The color resemblance of each Salix borer to the Populus borer living with it is close enough so that they were usually lumped as single western and eastern species prior to Fisher's revision. While granulatus populi and quadriguttatus niveiventris are iridescent reddish-cupreous above (the latter sometimes very dark), the nominate subspecies are duller, being more or less dusky olivaceous to reddish-fuscous. These pairs of Populus and Salix borers seem to be the most austral and least alpine of the forms in the triad composed of the Salix, Populus, and Alnus-Betula boring species.

The climatic affinities of anxius and g. liragus are quite boreal and alpine

by comparison. They are darkly pigmented, usually almost black, although the pronotum and vertex of anxius are apt to be cupreous, particularly in specimens from the northeastern U. S. A. and southeastern Canada. Fisher (1928) failed to distinguish anxius from g. liragus because they are very similar.

The similarities within any of the sympatric pairs, anxius and granulatus liragus, quadriguttatus niveiventris and granulatus populi, or nominate quadriguttatus and granulatus, are homoplastic¹, not homologous. They appear to be due to adaptation to similar or equivalent climatic conditions.

DISCUSSION

Faunal Connections. The gradual cooling of climate that occurred at the close of the Tertiary, particularly at higher latitudes, brought southward retraction of the Arcto-Tertiary flora and largely eliminated it from Europe (Spurr, 1964). Remnants of this forest persist in eastern Asia (Japano-Manchurian), Pacific coastal North American (Vancouverian), and eastern North America. North of these Arcto-Tertiary remnants, particularly in the more continental regions, the modern boreal forest associations were formed (Linsley, 1963). Logically, then, one looks to the Japano-Manchurian region for faunal connections with the Vancouverian and Alleghenian regions. Linsley (1963) shows that the cerambycid faunas of the latter two regions have separate connections with the former. Species bridging the gap between browni and horni or between the latter and criddlei may occur in the Japano-Manchurian region. In this same region one might also find pre-Quaternary connections with the non-boreal Salix and Populus borers of North America (cf p. 82). These non-boreal forms may be rather direct descendents of the pre-Quaternary forms which presumably gave rise to the boreal ones, such as the Populus borers, tamanukii of eastern Asia, and g. liragus of North America. Each of these boreal Populus borers could have had an independent origin but there is no necessity for assuming that it was so.

Linsley (1963) says that Holarctic cerambycid species dominate in the forests of such boreal derivatives of the Arcto-Tertiary Geoflora as the northern and high elevation Pinaceae, and the northern deciduous trees, especially Salix and Populus. There is a definite likelihood that tamanukii is conspecific with granulatus. In fact, tamanukii and g. liragus may represent derivatives of a single boreal form which might have persisted at the southern edge of the Bering Arc during late-Pleistocene glacial maxima.

Subspeciation. It is clear that g. liragus must have been isolated from g. granulatus and g. populi (or the g. granulatus-g. populi ancestor) in an area of colder climate, where it derived a more cold-adapted type of pigmentation and its affinity for a boreal climate. There is no logical explanation for isolation north of the g. granulatus-g. populi range unless it occurred as a result of glaciation or unless g. liragus was absent from North America and derived its boreal affinities in Asia, later migrating to North America through Beringia. In the latter case, the problem of isolation from Japano-Manchurian forms is raised.

According to Heusser (1965), macro-fossils, dated 35,000 B. P., from the unglaciated Alaskan interior, show that a forest of aspen, birch, and spruce persisted there throughout the Wisconsin glacial interval. This refugium seems to be the only northern Nearctic one (other than Vancouver Island) for which

¹“Homoplasy is resemblance not due to inheritance from a common ancestry (Simpson, 1956).”

there is good evidence of the survival of forests during the Wisconsin glacial maxima. This seems to be as likely a place as any for the derivation or reinforcement of the boreal affinities of g. liragus. As suggested above, another possible refugium is the southern edge of the Bering-Chukchi platform which was emergent during glacial maxima. Although most paleobotanists who have studied the problem suggest that forests never existed on the Bering land bridge, their views do not seem to be supported by the frequency of Holarctic distributions among boreal forest insects.

A. granulatus liragus occurs at the same latitudes with g. granulatus or g. populi in mountainous regions, and in these areas the former seems to be confined to higher altitudes, while g. granulatus or g. populi occur mostly in river bottoms at lower altitudes. Their coloration appears to be a genuine indication of their climatic affinities. Intergradation between g. liragus and the other subspecies should occur at intermediate altitudes where cottonwood (P. deltoides) or black cottonwood (P. balsamifera ssp. trichocarpa) occurs together with aspen (P. tremuloides).¹

One specimen from Crow Agency, Montana (July, 1916; R. K. Kellog), recorded under Agrilus granulatus by Fisher (1928), appears to represent an intergrade between g. granulatus and g. liragus, as its color is rather dark and the spots on the elytra are not as distinct as those of g. granulatus specimens from farther south. The Agrilus granulatus² discussed by Brown and Stevenson (1963) are very similar to the foregoing. It is interesting that the species of the various sections of the genus Populus hybridize in southern Alberta, where their habitats intergrade (Brayshaw, 1965). For g. granulatus and g. liragus this area seems to represent a natural counterpart of the "hybridized habitat" of Anderson (1948).

During the Pleistocene pluvials--the cool, moist periods when glaciation occurred--the ranges of willows and cottonwoods must have expanded from both east and west out into the southern Great Plains so that there was even less disjunction than occurs presently. Although they do not show Salix and Populus, the pollen analyses of Martin and Mehringer (1965) for the southwestern U. S., indicate that this is more than just a likelihood. Thus, the stage would have been set for movement of eastern Salix and Populus borers into the West and vice versa. Following continent-wide dispersal of these forms, there may have been a sequence of hypsithermal divergences followed by broad intergradations between eastern and western forms during pluvial periods. It is very likely that this occurred several times, as Deevey (1949) says that in the history of Lake Bonneville there have been two, perhaps three, major late-Pleistocene pluvials.

At the present time the ranges of g. populi and g. granulatus do not appear to interdigitate extensively. That of g. populi is western, extending from southern California to British Columbia and as far east as Missoula, Montana. The range of g. granulatus extends from the Great Plains eastward; although its limits are not well-known, Fisher recorded it from as far north as Nassau, New York, and as far west as Crow Agency, Montana, and south to Illinois and

¹Any Populus sp. or cultivar appears suitable for all of the subspecies of granulatus, provided that the former occur in habitats of the latter.

²Specimens from these rearings are deposited in the Canadian National Collection, Ottawa, Ontario.

Missouri, and there is one specimen from North Carolina in the Horn collection¹. In Colorado only g. granulatus is known, but some of the specimens² examined from that area show indications that the two probably meet and intergrade there in places.

The Salix borers q. quadriguttatus and q. niveiventris are known from farther south than their Populus-boring counterparts. The range of q. quadriguttatus extends roughly from Georgia³ to Texas, north to Colorado and east to Pennsylvania and Washington, D. C. The northern range limit of q. niveiventris lies just south of Placerville, California (see below) and, according to Van Dyke (1942), this subspecies ranges south into Baja California, and east into Arizona and New Mexico. Although we have seen no definite q. niveiventris-q. quadriguttatus intergrades, some q. quadriguttatus specimens are distinctly tinged with red, probably indicating recent genetic exchange with q. niveiventris. The divergence between these Salix borers was probably concurrent with that occurring between g. granulatus and g. populi.

Because of their color similarities, it appears that quadriguttatus niveiventris and granulatus populi were confined to regions with similar climates during their period of divergence (hypsithermal) from eastern allies. Their ranges at that time may have been more nearly coextensive than at present. Although q. niveiventris occurs in Baja California, Arizona, and New Mexico, g. populi has never been collected in these areas, in spite of the occurrence of Fremont cottonwood (Populus fremontii) in their stream bottoms. On the other hand, g. populi occurs undifferentiated well north of q. niveiventris, where quadriguttatus is represented by the more northern subspecies, q. fulminans.

According to Van Dyke (1942) some records for q. niveiventris from British Columbia may refer to q. fulminans, but this is not altogether certain because g. populi was not distinguished from q. niveiventris any sooner than q. fulminans. We are not aware of any reliable records for q. fulminans outside of those for Oregon and Northern California, and do not know how well-differentiated q. niveiventris and q. fulminans are. Unfortunately, Fisher (1928) described q. fulminans from a series of specimens which seem to represent intergrades⁴ between q. niveiventris and Salix borer populations north of the q. fulminans type locality. This series (q. fulminans type and paratypes) was taken at Placerville, California, and some specimens are iridescent reddish cupreous above, which seems fairly typical for q. niveiventris, while others are greenish. Fisher (1928) had specimens from Biggs and Castle Crags in California which were strikingly different from those collected farther south at Placerville. He

¹Philadelphia Academy of Sciences, Philadelphia, Pennsylvania.

²Personal collection S. G. Wellso, Dept. of Entomology, Michigan State University, East Lansing.

³Record in Franklin and Lund (1956).

⁴Fisher based his distinction of q. fulminans upon the efflorescent spots on the sides of the abdominal sternites, but this character does not seem to merit the value he has given it and may be more characteristic of the population at the type locality than of those elsewhere.

says, "the specimens from Biggs have the elytra dark green and the pronotum more bronzy green, and two specimens from Castle Crag¹, which I have placed under this species, have the pronotum greenish blue and the elytra a beautiful violaceous blue." Specimens were seen from Crescent Mills, California, in the northeastern part of the Sierra Nevada, that are bright apple-green. Barr² said he had examined relatively few specimens of this Pacific Northwest form, but those he had seen are green. Beer³ said q. fulminans specimens from northern California and Oregon are blue.

Some sort of past range disjunction must account for the color differences of q. niveiventris and q. fulminans. It may have occurred during a hypsithermal period, when the ancestral populations in the Cascades or northwestern coast ranges may have been isolated from those in the southern coast ranges or the Sierras. An alternative possibility is that the population that gave rise to q. fulminans may have been isolated in a Pacific Northwest glacial refugium, such as the one which, according to Heusser (1960), existed on Vancouver Island. The nature of the climatic affinities of q. fulminans may become clearer as more collections are made.

The Multiplication of Species

Speciation in the anxius Group. The only cases of complete speciation among the triad of the Populus, Salix, and Alnus-Betula borers that can, with reliability, be designated as Nearctic, Pleistocene events are those which led to the derivation of the ancestor of the latter and the subsequent formation of two siblings from it. Previously (page 80) we discussed the possible derivation of the ancestral form from a willow feeder. This may have occurred very early in the Pleistocene, and the point of origin may have been eastern North America. No species in the anxius group, other than its namesake, is known to live on a species of Betulaceae in the western part of the continent. However, Chamberlin (1924) says he collected a specimen of q. niveiventris on Oregon alder (Alnus rubra) near La Grande, Oregon, and that a series was collected on black cottonwood and Oregon alder at Oakridge, Oregon.

Following his description of g. populi, Fisher (1928) lists 4 of the paratypes as having been taken on Oregon alder by Chamberlin at Oak Ridge, Oregon⁴. The only one of these paratypes remaining in the collection of the U. S. National Museum has no host label. One in the Chamberlin collection at the California Academy of Sciences, was labeled "Oakridge VI-29 Ore./Populus trichocarpa/W. J. Chamberlin Collector⁵." Chamberlin (1929) described trichocarpae, a synonym of g. populi from the same series of Oak Ridge specimens, but he did

¹Emendation of his "Castle Crag."

²Personal communication, 1967; W. F. Barr, Dept. of Entomology, University of Idaho, Moscow.

³Personal communication, 1967; F. M. Beer, Dept. of Biology, School of Science, Oregon State University, Corvallis.

⁴Emendation of Fisher (1928) who cites Oak Ridge as a California locality.

⁵Personal communication, 1967; H. B. Leech, California Academy of Sciences, San Francisco.

not say any of these were collected on alder (cf above citation, Chamberlin, 1924). Beer and Hatch (1941) cite lombardy poplar, black cottonwood, and Oregon alder as g. populi hosts, but are, no doubt, following Fisher (1928).

Beer¹ doubts the existence of a western form resembling g. populi that infests Oregon alder. He has collected g. populi in places where alders and black cottonwoods had been felled simultaneously, but saw none on the alders. Moreover, he says, "Knowing Chamberlin's inaccuracies on host plants--in fact his general failure to mention this feature would prompt me to discount completely occurrence on this plant [alder]."

Evidently anxius has a greater specificity than pensus for hosts in a severely weakened condition, but anxius hosts are usually also larger and more likely to occur on xeric sites. A. pensus, then, appears to be more "primary" in its attacks on alders and young river birches than anxius is in attacking its hosts. There is no a priori reason for assuming that anxius would not be attracted to large felled or injured river birches, provided they were located in the right places. A number of birches appear to be satisfactory for anxius, and the alleged olfactory attractants, therefore, appear not to be so host-species-specific as they are specific to certain conditions of the host. On the other hand, there is no evidence to show that pensus is not attracted to such large felled or injured river birches, but without such evidence one must assume that it is not. It seems very necessary to hypothesize this and the other anxius-pensus differences proposed above, if one is to explain their discreteness in sympatry.

The distribution of Agrilus pensus suggests that it was confined to the Atlantic seaboard during the primordial stage of its evolution. The divergence of anxius and pensus may have occurred while the latter was confined to the glacial refugium known to have existed in the southeastern U. S. There is evidence showing that about 15 to 16 thousand years ago forests of birch and alder mixed with pine, spruce and fir, existed in the Dismal Swamp region of southeastern Virginia (Whitehead, 1965). Similar ecological conditions may have existed there during glacial ages prior to the Wisconsin so that the common ancestor of anxius and pensus may have diverged from a Salix-boring ancestor in the same refugium.

The ranges of pensus and anxius and also their color differences suggest that when they were geographically isolated they were exposed to different climatic conditions. Therefore, anxius may have been confined to a refugium west of the Appalachians in the south central U. S. Although there has been a great deal of dispute on this matter, it has become increasingly evident that during the Wisconsin, at least, boreal tree species occurred as far south as Louisiana and Texas (cf Deevey, 1949 and Whitehead, 1965).

Following its continent-wide dispersal, anxius may have had its range fractured during another glacial stage. Specimens from the East differ from western ones in having the vertex and pronotum more distinctly cupreous-colored. Specimens from the Upper Peninsula of Michigan may represent intergrades, as some are colored more like g. liragus, while the pronotum and vertex of others are quite distinctly cupreous-tinged. Townes² says it is not

¹Personal communication; see footnote 3, page 87.

²Personal communication, 1967; H. K. Townes, American Entomological Institute, Ann Arbor, Michigan.

unusual for intergrades between eastern and western subspecies of ichneumonflies to occur in that area. These east-west differences of anxius adults could relate to the fact that the only indigenous western birches of tree size are those of the paper birch group, which are mostly boreal. Because anxius occurs at least as far south as Washington, D. C. in the East, adults from the West, generally, may be more cold-adapted.

The Sibling Species Concept. Mayr (1963) defines sibling species as "morphologically similar or identical populations that are reproductively isolated." Certainly, anxius and g. liragus would be sibling species by that definition, but it is of little value if it fails to make a distinction between homoplasy¹ and homology. "The fundamental difference between the method of morphological and phylogenetic systematics is that the latter breaks up the simple concept of resemblances (Hennig, 1965)."

The archaic level of Agrilus classification is due to the relatively unsophisticated concepts of the classifiers, who usually have not tried to distinguish between homoplasy and homology. Those unaware of this fact tend to regard Agrilus and other large buprestid genera as being more unique than they really are. Mayr (1963) says:

Among the 25 species of Carabus beetles from central Europe, 80 percent are polytypic, while in certain well known genera of buprestid beetles not a single² species is considered polytypic. There are still large groups of animals in which all species are listed under binomials. It would be interesting to know to what extent this is due to lack of geographic variation in the phenotype and to what extent to insufficient taxonomic analysis. Sibling species, of course, are nearly always monotypic.

Although Obenberger (1957) claimed that the Buprestidae are taxonomically well-known, they certainly have not been studied nearly as intensively as the majority of Carabidae. Therefore, Mayr's comparison of buprestids and carabids is invalid. There appears to be no greater lack of geographical variation in the phenotypes of buprestids than in most other groups (see Obenberger, 1958). Binomial names are still preponderant over trinomials in Agrilus because much of the taxonomic work on that genus is old or has been done by species describers instead of classifiers. Some of it has also been done by people working on local faunas. The forms they call "sibling species, of course, are nearly always monotypic."

Mayr (1963) drew the following "conclusions concerning sibling species":

1. There is no sharp division between ordinary species and sibling species...
2. Sibling species, when subjected to a thorough analysis, usually are shown to differ in a whole series of minor morphological characters. Like ordinary species they are separated from each other by distinct gaps.
3. Sibling species are apparently particularly common in those kinds of animals in which chemical senses (olfactory and so on) are more highly developed than the sense of

¹Defined in footnote on page 84.

²Probably an overstatement of the case, with the possible exception of some smaller genera. However, Mayr (1963) does not appear to be referring to any of the smaller genera because they are obscure and because he elsewhere refers to Agrilus and Acmaeodera.

vision... Sibling species are apparently rarest in organisms such as birds that are most dependent on vision in the recognition of epigamic characters.

4. There is no indication that sibling species arise by a process of speciation different from that which gives rise to other species.

5. Degree of morphological similarity in sibling species is an indication not of genetic similarity, but rather of developmental homeostasis. A reconstruction of the genotype, resulting in the reproductive isolation of two species, can take place without visible effect on the morphology of the phenotype [cf number 2!].

6. Evolutionary changes in the genetic constitution seem to occur in groups of sibling species at the same rate as in groups of morphologically very distinct species.

The following paragraph from Mayr (1963) is certainly contradictory to numbers 4 and 6 of the conclusions listed above. He says:

In many groups of insects there are large genera with many species, each of which appears to be limited to a single host. Genera with essentially monophagous species have been described for microlepidoptera, solitary bees, buprestid beetles (*Acmaeodera*, *Agri-lus*), chrysomelid beetles (*Calligrapha*, *Arthrochlamys*), and other groups. Two phenomena in particular seem to suggest a mode of speciation in these food specialists that is different from speciation in most other animals. The first is that monophagous insects often, if not usually, belong to large genera. It is argued that sympatric speciation permits more rapid and more frequent speciation than geographical speciation. It would seem even more plausible, however, that the great number of congeneric species is due to the vastly increased number of available niches and the reduction of competition. Likewise, high food specificity should greatly enhance the efficiency of eco-geographical barriers.

Mayr seems to make analogies with speciation among insular birds, and in doing so does not seem to be in complete accord with number 3 of his conclusions about sibling species. He claims that:

As in all speciating animals the crucial events are apt to take place in peripherally isolated populations and these have not been studied adequately in even a single one of the groups of monophagous species. As a working hypothesis one might assume that a subsidiary host may offer more favorable conditions under the changed ecological situation of the marginal environment (fig. [47]). The shift from one host to another will set up an increased selection pressure that will result in rapid genetic alteration of the population. The amount of genetic variability appears to be low in a species that has been adapted for life on a single host. Host specificity is thus an ideal prerequisite for rapid speciation.

A narrow-ranged host specificity certainly is low variability per se, but does not necessarily reflect low genetic variability. There seems to be no reason to assume that host specificity differs basically from other phenotypic aspects. Relatively invariable host specificities, therefore, may be a consequence of homeostasis or coadaptation of the gene pool. "The real problem in speciation is not how to produce a difference but rather how to escape from the cohesion of the gene complex. No one will comprehend how formidable a problem this is who does not understand the power of the cohesive forces that are responsible for the coadapted harmony of the gene pool [Mayr, 1963]." As far as we know, the problem of breaking away from gene pool coadaptation is greatest for species with a narrow range of host specificity because the cohesiveness of their gene pools may be greatest.

It appears that in the anxious group species which have highly specialized relationships to their hosts in a given respect (i. e. to species, size, physiological condition, etc.) may usually evolve from less specialized species or from

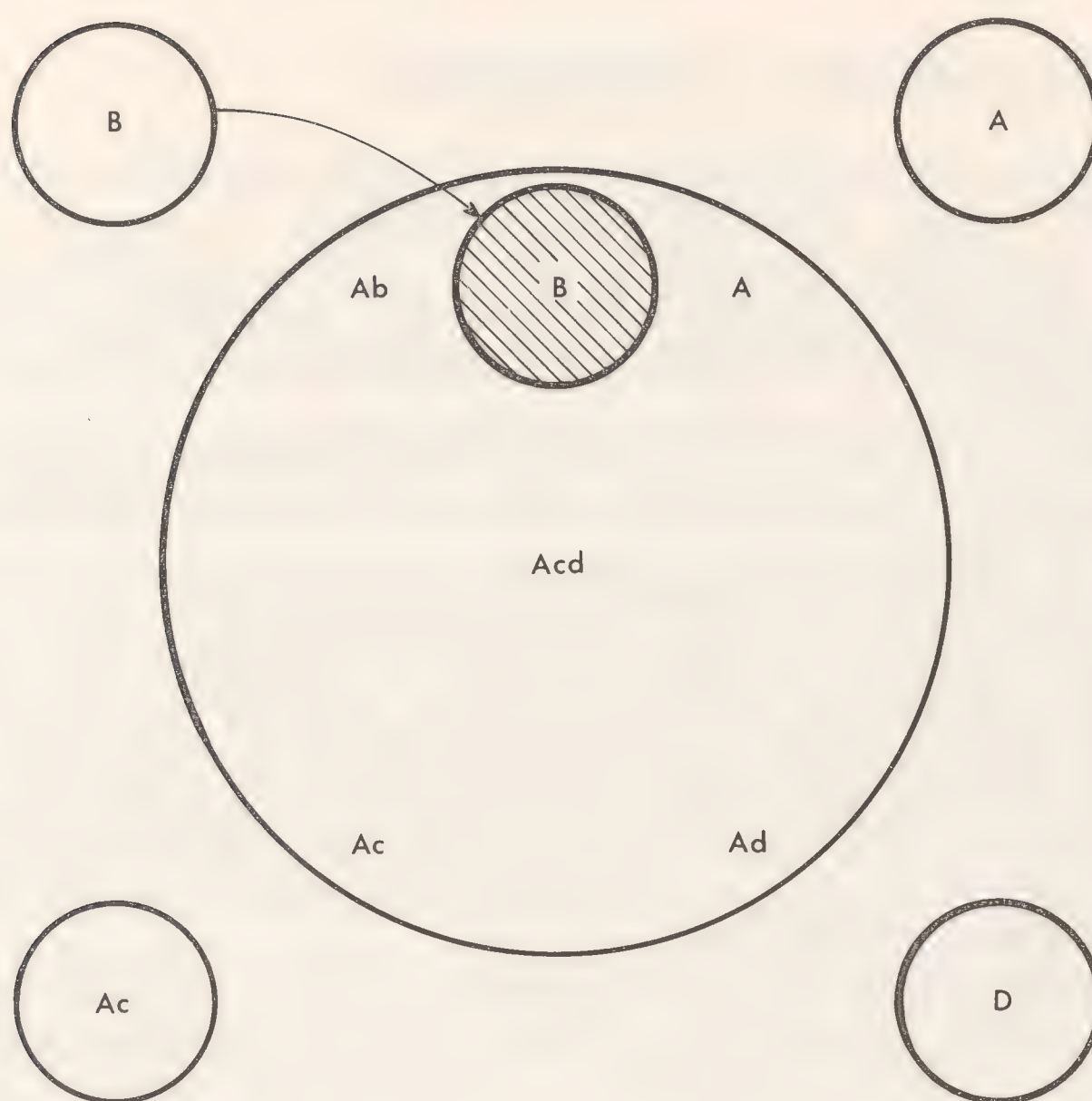


Fig. 47. Primary hosts (capital letters) and subsidiary hosts (small letters) of an essentially host-specific species. The large circle indicates the main range of the species; the outlying small circles, the peripheral isolates. New primary hosts (B, D) are acquired in some peripheral isolates, facilitating subsequent speciation. Reinvasion from the isolate that is host specific for B will establish a new species (hatched area) if reproductive isolation had been acquired during the geographic isolation (legend as in Mayr, 1963; figure redrawn).

species specialized in a different way. The most recent (mid- to late-Pleistocene) instances of complete speciation which seem to have occurred among the Populus, Salix, and Alnus-Betula borer groups (fig. 44, above) are those in which an Alnus-Betula boring species evolved from a Salix borer and subsequently gave rise to pensus and anxius. While anxius has evolved the greater specificity to physiological host condition, pensus appears to be more specific to host size.

One does not need a special working hypothesis for explaining these speciations. It is most plausible to attribute them to the events of the Pleistocene, in particular glaciation, which undoubtedly gradually severed ancestral stocks and left the disjunct populations with ranges that probably became separated farther and farther and increasingly different in climate.

Mayr's model (fig. 47) does not seem to provide for geographic separation sufficiently great to result in the climatic differences that seem to have been precursory to speciation in the anxius group, at least, nor does it seem to allow enough time for the occurrence of these climatic differences and for the reconstruction of the genotype. Perhaps in groups for which rapid speciation is a credible assumption, this model will prove to be worth considering. Most of the large groups will require a good deal more study before it will be possible to assert that conventional hypotheses are not as plausible in specific cases

as are hypotheses providing for rapid speciation.

Evolutionary Synopsis

The reader is referred to figure 44 (p. 75) for a general summarization of the relationships between the forms in the Agrilus anxius group. The important points are these:

1) There appears to be no direct relationship between horni and anxius; while horni is probably most directly allied to forms like browni, pensus is the closest ally of anxius.

2) The major difference between horni and anxius (and allies of the latter) relates to the distinctness of their modes of (hypothesized) host selection. A. horni appears to rely upon a stem "measuring" mechanism in limiting the placement of its eggs to aspen suckers of particular sizes (but apparently without any discrimination in relation to their physiological condition). On the other hand, anxius oviposits on hosts that are in a decrepit physiological state and is apparently attracted to them by odiferous by-products of the bio-chemical breakdown associated with their decrepitude.

3) Forms linking these two distinct modes of life are found in pensus or quadriguttatus (and its subspecies). These species are apparently less specific to host condition and more specific to host size than anxius, although probably more reliant upon a subnormal state of host physiology than horni.

4) A. quadriguttatus and guerini probably descended from a single phyletic line, and the latter seemingly has developed some significant morphological modifications from the usual Salix borer type. These Salix borers appear to share common ancestry with: (a) criddlei, a gall-former living on willow, which may in turn be somewhat related to horni, (b) a line of Populus borers including the Palearctic ater and Nearctic granulatus, and (c) anxius and pensus, through a later derivation independent of that for the Populus borer group.

5). The sibling species concept has been applied far too indiscriminately in advance of a thorough assessment of the relationships among species, and this is certainly pertinent to many groups besides Agrilus. The following pairs have often been related by homoplasy (similarity) rather than homology: anxius and g. liragus; g. granulatus and q. quadriguttatus; or granulatus populi and quadriguttatus niveiventris.

6) The only recent speciations that seem evident for the Populus, Salix and Alnus-Betula borer groups are the derivation and subsequent splitting of an anxius-pensus common ancestor.

7) No special models are needed to explain these speciations or the subspeciations that have occurred in quadriguttatus (Nearctic Salix borers) or granulatus (Nearctic Populus borers). They can logically be related to biogeographical events of the Pleistocene.

SUMMARY

The principal objective of this study was to assess the relationship between A. anxius, A. pensus, A. granulatus liragus, and A. horni. This was accomplished by: (1) studying specimens, (2) assembling what was known about general aspects of their biology, augmenting it in places with new observations, (3) making behavioral observations on the adults in the field and laboratory, and (4) analyzing their phylogeny and zoogeography, relying heavily on material from the preceeding sections.

In the process of studying the taxonomy of the adults, the need for a number of nomenclatural changes became apparent. Changes which were made very recently (see Carlson, 1969) include lowering four taxa from species to subspecies status (populi and liragus to ssp. of granulatus, niveiventris and fulminans to ssp. of quadriguttatus) and the suppression of two names, betulae and nevadensis as synonyms of pensus and q. niveiventris, respectively. Herein lateralis is suppressed as a synonym of ruficollis, and the species which has been incorrectly called lateralis is named browni.

Barter and Brown (1949) distinguished g. liragus from anxius, but thought horni to be a probable synonym of the latter. After Harrison (1959) had discovered horni boring in the roots of aspen suckers, Nord et al. (1965) established its identity and showed that horni was clearly distinct from either anxius or g. liragus.

A careful comparison of the adults revealed that horni has some previously unnoticed or unemphasized morphological traits which, although they are subtle, set it apart from anxius or g. liragus. They are discussed at some length in the taxonomy section and again in the evolution section, where their significance is assessed.

These anomalous morphological characteristics of horni seemed to link it in some way with species which lack prehumeral carinae. A paper by Fisher (1922), completely overlooked until late in this study revealed that the habits of A. browni are remarkably like those of horni. The morphological traits separating horni and anxius or g. liragus and linking it with other forms, not closely related to the latter, thus became more meaningful. The important ways in which the habits of horni differ from those of anxius or g. liragus are enumerated below.

1) The eggs of horni are deposited at the bases of young aspen suckers, while suitable oviposition sites for g. liragus and anxius occur almost anywhere along the stems of larger trees.

2) After hatching the horni larvae bore into the phloem and proceed downward to a root and move rather directly out along it for a distance of up to 3 1/2 feet before the first molt occurs. This primary molt probably does not occur until the spring following eclosion from the egg, when the larvae may begin spiraling back toward the sucker stem. The first molt of anxius or g. liragus larvae occurs soon after the larvae bore into the phloem.

3) In many cases the larvae of anxius and g. liragus complete their development and form a pupal chamber during the same year in which eggs are laid. They thus have a one-year life cycle under some conditions and a two-year cycle under others. The usual length of life cycle is two years for horni, and the only exception that seems possible, is an occasional three-year cycle.

4) While anxius and g. liragus infest hosts that are under physiological stress and seem to be attracted to them by odiferous products of biodegradation, horni appears to distinguish suitable from unsuitable hosts on the basis of size rather than their physiological condition. The suckers on which horni

eggs are found seem to be of normal vigor (i. e., no different than their neighbors). Sucker diameter (as opposed to height) appears to be the most important variable correlating with the occurrence of eggs. It is, therefore, suggested that horni restricts its egg deposition to suckers within rather narrow diameter limits (0.3 to 0.9 inches at base) by thigmotactic means. The differences between the two kinds of host selection seem to be so extensive as to preclude the derivation of one from the other except through a series of intermediate stages.

Agrilus pensus seems to be a direct descendant of an ancestor representing one of the intermediate stages. A two-year life cycle seems prevalent, and a one-year cycle is unlikely because of the small size and thin bark of its hosts (alders and young river birches). A. pensus is probably more primary than anxius or g. liragus, although it seems likely that the hosts it attacks are under some physiological stress. Nevertheless, the average level of host resistance which pensus is subjected to should approximate the maximum encountered by anxius or g. liragus.

Host resistance is treated here as a population regulating factor, together with parasites and predators. The sinuate galleries of anxius and zigzag galleries of g. liragus appear to be mechanisms for coping with host resistance, because the galleries of either species follow a more random course in the phloem of hosts that have succumbed or are near death.

The survival of horni larvae may depend, in part, upon the ability to lower the vigor of the host through root-girdling. Their ability to significantly lower the vigor of the host by root-girdling should relate to root diameter. Because root diameter seems to correlate well with sucker diameter, the restriction of oviposition by horni to suckers with basal diameters ordinarily below 0.9 inches is probably an indirect means for coping with host resistance.

The effects of parasites and predators as population regulating factors is more obvious, and for this reason, their significance may be overrated in comparison with that of host resistance. Woodpeckers and egg-parasitizing chalcidoids account for the greatest percentage of combined parasite and predator effects upon populations of anxius and g. liragus. The eggs of horni are parasitized rather infrequently, but larval parasites consume a very high percentage (about 42 percent) of horni brood between the late larval and late pupal stages. Some corrections are made regarding incorrect parasite rearing records.

Even though horni and g. liragus live on the same host species there appears to be no chance for interspecific mating because the males of each orient to hosts that are likely to be attractive to conspecific females. Moreover, horni females are completely unreceptive to liragus males, at least in the laboratory, and this seems to partially preclude hybridization in chance encounters. It appears, that g. liragus males have lost some subtle facet from their courtship behavior repertoire. A. anxius females are occasionally receptive to g. liragus males, but horni females, nevertheless, seem quite receptive to anxius males. This seems to put the male-to-female communications of anxius somewhere intermediate between those of g. liragus and horni, as horni males are accepted readily by females of either anxius or g. liragus. A. anxius could be intermediate in this respect because of the relative propinquity of its ancestry to species that live on willows as compared to that of g. liragus.

Males show no disinclination to court females of other species in the laboratory. Moreover, males do not even appear to recognize the sex of the individuals they court until they have made physical contact with them. Sexual

recognition by males appears to depend upon the structure of the courted individual's last abdominal segment. That segment is sexually dimorphic, and after a courting male probes it with his aedeagus he leaves males but prolongs courtship even with unreceptive females. This seemingly inefficient mode of sexual recognition appears to be homostatically tied to a dispersing function for homosexual encounters between the quasi-territorial males.

The interpretation presented here concerning evolutionary relationships within the Agrilus anxius group, contrasts with views held by earlier students. For example, horni is not considered as being a close ally of anxius or granulatus liragus. A. horni and browni have very similar habits, and these species appear to be more closely related to each other than to other species. This interpretation leaves a distinct phyletic gap between horni and anxius or g. liragus. Intermediates which seem to fill this gap are criddlei and a group of willow boring species that includes quadriguttatus. The ancestors of the latter group seem to have given rise first to a phyletic line that includes g. liragus and later to one including both anxius and pensus. The derivation of the line including anxius and pensus, and its subsequent splitting seem to be the only recent (mid- to late-Pleistocene) cases of complete speciation for the part of the anxius group considered in detail.

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LITERATURE CITED

- Alexander, R. D., T. E. Moore, and R. E. Woodruff 1963. The evolutionary differentiation of stridulatory signals in beetles (Insecta: Coleoptera). *Anim. Behav.* 11: 111-115.
- Alexeev, A. V. 1960. On the morphology and systematics of larvae of some species of Agrilus Curt. in the European part of U. S. R. R. *Zool. Zhur.* 39: 1497-1510, Eng. Summ.
- Anderson, E. 1948. Hybridization of the habitat. *Evolution* 2: 1-9.
- Anderson, R. F. 1944. The relation between host condition and attacks by the bronzed birch borer. *J. Econ. Entomol.* 37: 588-596.
- Arru, G. M. 1962. The influence of soil conditions on the vulnerability of the poplar to Agrilus viridis L. var. populnea Schaef. (Coleoptera: Buprestidae) in northern Italy. *World For. Congr. Proc.* 5: 948-950, Fr., Eng. Summ.
- Balch, R. E. and J. S. Prebble 1940. The bronze birch borer and its relation to the dying of birch in New Brunswick forests. *For. Chron.* 16: 179-201.
- Barter, G. W. 1957. Studies of the bronze birch borer, Agrilus anxius Gory, in New Brunswick. *Canad. Entomol.* 89: 12-36.
- _____. 1965. Survival and development of the bronze poplar borer, Agrilus liragus Barter & Brown (Coleoptera : Buprestidae). *Canad. Entomol.* 97: 1063-1068.
- _____. and W. J. Brown 1949. On the identity of Agrilus anxius Gory and some allied species (Coleoptera : Buprestidae). *Canad. Entomol.* 81: 245-249.
- _____. and D. G. Cameron 1955. Some effects of defoliation by the forest tent caterpillar. *Canada Dept. Agr., For. Biol. Div., Bi-Monthly Prog. Rept.* 11 (6): 1.
- Basurmanova, O. K. 1958. Biological forms of Agrilus viridis L. *Zool. Zhur.* 37: 1039-1044, Eng. Summ.
- Beer, F. M. and M. H. Hatch 1941. The Coleoptera of Washington: Buprestidae. *Univ. Wash. Pub. in Biol.* 10: 93-142.
- Benoit, P. 1965. Morphologie larvaire des Agrilus liragus Barter et Brown et Agrilus anxius Gory (Coleoptera: Buprestidae). *Canad. Entomol.* 97: 768-773.
- Bier, J. E. 1964. The relation of some bark factors to canker susceptibility. *Phytopath.* 54: 250-253.
- Blanchard, F. 1889. A list of the Buprestidae of New England. *Entomol. Amer.* 5: 32.
- Brayshaw, T. C. 1965. Native poplars of southern Alberta and their hybrids. *Canad. Dept. For. Pub. no.* 1109, 40 p.
- Britton, W. E. 1922. The bronze birch borer (22nd Rept. of the State Entomologist for 1922). *Conn. Agr. Exp. Sta. Bul.* 247: 359-361.
- Brooks, F. E. 1914. The apple root borer. *J. Agr. Res.* 3: 179-185.

- Brown, C. E. and R. E. Stevenson 1963. Forest insect conditions in Alberta. Ann. Rept. For. Ins. and Dis. Surv., For. Entomol. and Pathol. Br., Canada Dept. For., for 1963, p. 100.
- Burks, B. D. 1967. In: Hymenoptera of American north of Mexico, synoptic catalog. U. S. Dept. Agr., Agr. Monogr. no. 2, suppl. 2, K. V. Krombein and B. D. Burks, eds., p. 268.
- Burril, T. J. 1890. The lombardy poplar borer, Agrilus granulatus Say. In: 5th Rept. U. S. Entomol. Comm. (House Misc. Doc., vol. 41), A. S. Packard, ed. pp. 443-444.
- Buxton, P. A. 1924. Heat, moisture, and animal life in deserts. Proc. Royal Soc. Lond. (ser. B) 96: 123-131.
- Carlson, R. W. 1968. Biology, taxonomy, and evolution of four sympatric Agrilus beetles (Coleoptera: Buprestidae). Ph. D. dissertation, Univ. of Michigan, Ann Arbor, 232 p.
- _____ 1969. Title as in Carlson (1968). Diss. Abstr. 29: 2930B.
- Chamberlin, W. J. 1924. Notes on the Buprestidae of Oregon with descriptions of n. sp. J. N. Y. Entomol. Soc. 32: 185-194.
- _____ 1929. Remarks on Buprestidae (Coleoptera) of the North Pacific Coast Region with descriptions of new species. Pan-Pac. Entomol. 5: 109-116.
- Chittendon, F. H. 1898. A destructive borer enemy of birch trees, with notes on related species. U. S. Dept. Agr., Div. Entomol. Bul. (n.s.) 18: 44-51.
- _____ 1900. Food plants and injury of North American species of Agrilus. U. S. Dept. Agr., Div. Entomol. Bul. (n.s.) 22: 64-68.
- Cook, A. J. 1890. The willow buprestid (Agrilus torpidus). Rept. Mich. State Bd. Agr. 29: 102-128.
- Cottrell, C. B. 1964. Insect ecdysis. In: recent advances in insect physiology, vol. 2, J. W. L. Beament, J. E. Treherne, and V. B. Wigglesworth, eds. Academic Press, London, pp. 175-218.
- Davis, D. W. and N. N. Raghuvir 1964. The biology of the rose stem girdler, Agrilus rubicola communis, on raspberries in Utah (Coleoptera : Buprestidae). Ann. Entomol. Soc. Amer. 57: 154-159.
- Davis, G. C. 1891. Notes on a few borers. Insect Life 4: 64-67.
- Davis, G. C. 1892. Notes on a few borers. 22nd Ann. Rept. Entomol. Soc. Ont., pp. 80-82.
- Deevey, E. S. 1949. Biogeography of the Pleistocene. Bul. Geol. Soc. Amer. 60: 1315-1416.
- Dejean, Comte P. F. M. A. 1833. Catalogue des Coléoptères de la collection de la collection de M. le comte Dejean, pt. 1. Méquignon-Marvis, Paris, 96 p.
- _____ 1836. Catalogue des Coléoptères de la collection de M. le comte Dejean, 3rd edit., pt. 1-4. Méquignon-Marvis, Paris, 384 p.
- Dobzhansky, Th. 1933. Geographical variation in lady-beetles. Amer. Nat. 67: 97-126.
- _____ 1956. What is an adaptive trait? Amer. Nat. 90: 337-347.

- Engel, R. L. 1968. Some comparative observations on the biology and habits of four species of the genus Agrilus (Coleoptera : Buprestidae). Unpublished M. F. Thesis, Univ. of Michigan, Ann Arbor, 38 p.
- Esau, K. 1953. Plant anatomy. John Wiley and Sons, Inc., New York, 735 p.
- Fabricius, J. C. 1787. Mantissa Insectorum I: 184-185.
- Fisher, W. S. 1922. Notes on Agrilus lateralis Say (Coleop.). Proc. Entomol. Soc. Wash. 24: 124-125.
- _____. 1928. A revision of the North American species of buprestid beetles belonging to the genus Agrilus. U. S. Nat. Mus. Bul. 145, 347 p.
- Fowler, R. F. 1963. Vigor and density of aspen suckers and attack by Agrilus n. sp. Unpublished M. F. thesis, Univ. of Mich., Ann Arbor, 42 p.
- Franklin, R. T. and H. O. Lund 1956. The Buprestidae (Coleoptera) of Georgia. Ga. Agr. Exp. Sta. Tech. Bul. (n.s.) 3, 48 p.
- Frost, C. A. 1912. New species of Coleoptera of the genus Agrilus. Canad. Entomol. 44: 250-252.
- Gaudin, L. 1921. Captures de Coléoptrès de France. Bul. Soc. Entomol. Fr. 1921: 114-116.
- Gory, H. 1841. Supplement Buprestidae. Vol. 4 of: Histoire et Incongraphie des Insects Coleopteres, by F. L. Laporte de Castelnau and H. Gory. P. Duménil, Paris, 356 p.
- Graham, K. 1959. Release by flight exercise of a chemotropic response from photopositive domination in a scolytid beetle. Nature 184: 283-284.
- _____. 1961. Air swallowing: a mechanism in photo reversal of the beetle Trypodendron lineatus. Nature 191: 519-520.
- Graham, S. A., R. P. Harrison, and C. E. Westell, Jr. 1963. Aspens, phoenix trees of the Great Lake Region. Univ. of Mich. Press, Ann Arbor, 272 p.
- Hall, R. C. 1933. Post-logging decadence in northern hardwoods. Univ. of Michigan Sch. For. and Cons. Bul. 3, 66 p.
- Harlow, W. M. and E. S. Harrar 1958. Textbook of dendrology, 4th ed. McGraw-Hill Book Co., Inc., N. Y., 561 p.
- Harris, T. W. 1829. Contributions to entomology VII. New England Farmer 8 (1): 2-3.
- Harrison, R. P., Jr. 1959. Insects and diseases of aspen. Ph. D. dissertation, Univ. of Michigan, Ann Arbor, 259 p.
- Heering, H. 1956. Zur Biologie, Ökologie und zum Massenwechsel des Buchenprachtkäfers (Agrilus viridis L.). Ztsch. Angew. Entomol. 38: 250-287; 39: 76-114.
- Hennig, W. 1965. Phylogenetic systematics. Ann. Rev. Entomol. 10: 97-116.
- Heusser, C. J. 1960. Late-Pleistocene environments of North Pacific North America. Amer. Geogr. Soc. Spec. Pub. no. 35, 308 p.
- _____. 1965. A Pleistocene phytogeographical sketch of the Pacific Northwest and Alaska. In: The Quarternary of the United States, H. E. Wright and D. G. Frey, eds. Princeton Univ. Press, Princeton, N. J., pp. 469-483.

- Hitchcock, C. L., A. Cronquist, M. Owenby, and J. W. Thompson 1964. Vascular plants of the Pacific Northwest, part 2. Univ. of Wash. Press, Seattle. 597 p.
- Horion, A. 1950. Diskontinuerliche Ost-West Verbreitung mitteleuropäischen Käfer. Proc. 8th Int. Congr. Entomol., Stockholm, pp. 408-417.
- _____. 1955. Faunistik der mitteleuropäischen Käfer, vol. 4 Kommissionverlag, Erwald Reitter, Munich, 280 p.
- Horn, G. H. 1891. The species of Agrilus of boreal America. Trans. Amer. Entomol. Soc. 18: 277-336.
- Hutchings, C. B. 1923a. Some biological observations on the bronze birch borer, Agrilus anxius Gory. 15th Ann. Rept. Quebec Soc. Prot. Plants (1922-1923), pp. 89-92.
- _____. 1923b. Some notes on the biology of two buprestids infesting blackberry and hazel. 53rd Ann. Rept. Entomol. Soc. Ont., pp. 43-46.
- Kalmus, H. 1941. Physiology and ecology of cuticular color in insects. Nature (London) 148: 428-431.
- Kangas, E. 1942a. Agrilus ater L., als Espenschädling in Finland. Ztsch. Angew. Entomol. 28: 359-365.
- Kangas, E. 1942b. Forstentomologische Studien an der Espe. Ann. Entomol. Fennici 8: 49-71.
- Kennedy, J. S. and C. O. Booth 1963. Coordination of successive activities in an aphid. The effect of flight on the settling responses. J. Exp. Biol. 40: 351-369.
- Kerremans, C. 1900. Buprestides nouveaux et remarques synonymiques. Ann. Soc. Entomol. Belg. 44: 282-351.
- Kessler, G. 1958. Zur Characterisierung der Siebröhrenkallose. Ber. Schweiz. Bot. Ges. 68: 5-43.
- Knight, F. B. 1958. The effects of woodpeckers on populations of the Engelmann spruce beetle. J. Econ. Entomol. 51: 603-607.
- _____. and W. Albertin 1966. Portable X-ray equipment: a useful tool in forest entomological field research. Pap. Mich. Acad. Sci., Arts, and Let. 51 (pt. 1): 23-26.
- Knull, J. N. 1922. Annotated list of the Buprestidae of Pennsylvania (Coleoptera). Canad. Entomol. 54: 79-86.
- _____. 1930. Notes on Coleoptera, No. 2. Entomol. News 41: 82-86.
- _____. 1934. Notes on Coleoptera, No. 4. Entomol. News 45: 207-212.
- _____. 1950. In: Insect enemies of eastern forests, F. C. Craighead, ed. U. S. Dept. Agr. Misc. Pub. 657: 187-188.
- Kramer, P. J. and T. T. Kozlowski 1960. Physiology of trees. McGraw-Hill Book Co., Inc., New York, 642 p.
- Kozlowski, T. T. 1964. Water metabolism in plants. Harper and Row, Pub., New York, 227 p.

- Krogerus, R. 1922. Studien über Agrilus-Arten, I und II. Not. Entomol. (Helsinki) 2: 10-14, 109-113.
- Kurosawa, Y. 1954. Buprestid fauna of eastern Asia (2). Tokyo Nat. Sci. Mus. Bul. (n.s.) 1: 82-93.
- _____. 1956. Buprestid fauna of eastern Asia (3). Tokyo Nat. Sci. Mus. Bul. (n.s.) 3: 33-41.
- Larsen, J. 1901. A disease of the white birch. 3rd Rept. Michigan Acad. Sci., Arts, and Let., pp. 46-49.
- Lecomte, C. 1925. Sur quelques Coleoptères obtenus d'élevages. Bul. Soc. Entomol. France, pp. 294-296.
- Leconte, J. L. 1859. Revision of the Buprestidae of the United States. Trans. Amer. Phil. Soc. (2nd ser.) 11: 187-258.
- Lindroth, C. H. and E. Palmén 1956. In: Taxonomist's glossary of genetalia in insects, S. L. P. Tuxen, ed. E. Munksgaard, Copenhagen, pp. 69-76.
- Linsley, G. E. 1963. Bering Arc relationships of Cerambycidae and their host plants. In: Pacific Basin biogeography, a symposium of the Tenth Pac. Sci. Congr. (1961), J. S. Gressitt, ed. Bishop Museum Press, Honolulu, pp. 159-178.
- Lintner, A. J. 1889. Fifth report on injurious and other insects of New York. 42nd Rept. N. Y. State Mus., p. 317.
- Lundberg, S. 1962. Contribution to the knowledge of Swedish Coleoptera 5, Agrilus guerini Lac. Entomol. Tidskr. 83 (3/4): 172-174, Sw.
- Manee, A. H. 1913. Observations on Buprestidae at Southern Pines, North Carolina. Entomol. News 24: 167-171.
- Martin, P. S. and P. J. Mehringer, Jr. 1965. Pleistocene pollen analysis and biogeography of the Southwest. In: The Quarternary of the United States, H. E. Wright and D. G. Frey, eds. Princeton Univ. Press, Princeton, N. J., pp. 433-451.
- Mayr, E. 1963. Animal species and evolution. Belknap Press, Harvard Univ., Cambridge, Mass., 797 p.
- Megerle von Mühlfeld, J. K. 1823. In: Coleoptera und Lepidoptera, ein systematisches Verzeichniss mit beigesetzten Preissen der Vorräthe, G. Dahl, ed. Vienna, Akkermann, pp. 19-20.
- Mundinger, F. G. 1941. Two buprestid cane-borers of brambles with experiments on control. J. Econ. Entomol. 34: 532-537.
- Nash, R. W., E. J. Duda, and N. H. Gray 1951. Studies on extensive dying, regeneration, and management of birch. Maine For. Serv. Bul. 15, 82 p.
- Netolitzky, F. 1831. Einige Regeln in der geographischen Verbreitung geflügelten Käferrassen. Biol. Zentralbl. 51: 277-290.
- Nord, J. C. 1962. A biological study of a new species of Agrilus (Coleoptera: Buprestidae) Unpublished M. F. thesis, Univ. of Michigan, Ann Arbor, 61 p.

- Nord, J. C., F. B. Knight, and G. B. Vogt 1965. Identity and biology of an aspen root girdler, Agrilus horni. For. Sci. 11: 33-41.
- Obenberger, J. 1957. Quelques considérations sur les sous-genre Epinagrilus v. Stepanov et sur les caractères du genre Agrilus Curtis en général (Col. Bupr.). Sb. Entomol. Oddel. Narod. Mus. v Praz (Acta. Entomol. Mus. Nat. Pragae) 31: 77-89.
- _____. 1958. Sur les relations entre les Buprestides de la région paléarctique et néarctique. Proc. Tenth Intern. Congr. Entomol. (1956) 1: 213-216.
- _____. 1959. Sur les espèces du genre Agrilus Curtis de l'Australie et Océanie (Coleoptera, Buprestidae). Sb. Entomol. Oddel. Narod. Mus. v Praz (Acta. Entomol. Mus. Nat. Pragae) 33: 233-240.
- Ohgushi, R. 1963. Development of ovary and pre-oviposition period of citrus flat-headed borer, Agrilus auriventris auriventris S. Saunders under laboratory conditions. Jap. J. Appl. Entomol. Zool. 7: 92-96, Jap., Eng. summ.
- Saunders, E. 1871. Catalogus Buprestidarum, p. 126.
- Say, T. 1823. Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains. J. Acad. Nat. Sci. Philadelphia 3: 139-216.
- Schaefer, L. 1949. Buprestides de France. Misc. Entomol., suppl., 511 p.
- Semenov-Tian-Shanskij, A. 1935. Analecta coleopterologica. Entomol. Obozrenie (Rev. d'entomol. U. R. S. S.) 35: 276, Latin.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., Inc., New York, 312 p.
- Smith, J. B. 1892. Notes on blackberry borers and gall-makers. Insect Life 4: 27-30.
- Smith, S. G. 1949a. Evolutionary changes in the sex chromosomes of Coleoptera. Nature (London) 164: 237-238.
- _____. 1949b. Evolutionary changes in the sex chromosomes of Coleoptera I. Wood borers of the genus Agrilus. Evolution 3: 344-357.
- Spaulding, P. and H. J. MacAloney 1931. A study of organic factors concerned in the decadence of birch on cut-over lands in northern New England. J. Forestry 29: 1134-1149.
- Spurr, S. H. 1964. Forest ecology. Ronald Press, New York, 352 p.
- Stäger, R. 1923. Ein Schädling der Himbeerkulturen. Schweiz. Entomol. Anz. 2: 21-22, 25-26, 29-30, 33-35.
- Stepanov, V. N. 1954. Two species of the genus Agrilus Curt. subgenus Epinagrilus sub-gen. nov., new to the fauna of the USSR. Zool. Zhur. 114-119.
- Swaine, J. M. 1918. A new forest insect enemy of white birch. Canad. J. For. 14: 1928-1929.
- Tanner, V. M. 1927. A preliminary study of the genitalia of female Coleoptera. Trans. Amer. Entomol. Soc. 53: 5-50.
- Tatewaki, M. 1963. Phytogeography of the islands of the North Pacific Ocean. In: Pacific Basin biogeography, a symposium of the Tenth Pac. Sci. Congr. (1961), J. L. Gressitt, ed. Bishop Museum Press, Honolulu, pp. 23-28.

- Théry, A. 1942. Faune de France Volume 41, Coleoptères Buprestides. Paul Lechevalier, Paris, 221 p.
- Townes, H. K. Jr. 1944. A catalogue and reclassification of Nearctic Ichneumonidae. Mem. Amer. Entomol. Soc. 11, pt. 1, 477 p.
- Townes, H. K. and M. Townes 1951. In: Hymenoptera of America north of Mexico, a synoptic catalog. C. F. W. Muesebeck, K. V. Krombein and H. K. Townes, eds. U. S. Dept. Agr., Agr. Monogr. no. 2, pp. 184-410.
-
1960. Ichneumon-flies of America north of Mexico 2. Subfamilies Ephialtinae, Xoridinae, and Acaenitinae U. S. Nat. Mus. Bul. 216, pt. 2, 676 p.
-
1962. Ichneumon-flies of America north of Mexico 3. Subfamily Gelinae, tribe Mesostenini. U. S. Nat. Mus. Bul. 216, pt. 3, 602 p.
- U. S. Weather Bureau 1964. Climatological data for Michigan (1964).
- VanDyke, E. C. 1942. Contributions toward a knowledge of the insect fauna of Lower California (Coleoptera: Buprestidae). Proc. Cal. Acad. Sci. 24: 97-132.
- Vité, J. P. 1961. The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in Pinus ponderosa. Contr. Boyce Thompson Inst. 21: 37-66.
- Walton, R. R. 1951. Control of the red-necked cane borer on prostrate brambles by summer pruning. J. Econ. Entomol. 44: 950-954.
- Whitehead, D. R. 1965. Palynology and Pleistocene phytogeography of unglaciated eastern North America. In: the Quarternary of the United States, H. E. Wright and D. G. Frey, eds. Princeton Univ. Press, Princeton, N. J., pp. 417-432.
- Wigglesworth, V. B. 1964. The hormonal regulation of growth and reproduction in insects. In: recent advances in insect physiology, vol. 2, J. W. L. Beament, J. E. Treherne, and V. B. Wigglesworth, eds. Academic Press, London, pp. 247-336.
- Wong, H. R. and B. B. McLeod 1965. The host and distribution of Agrilus criddlei Frost in Canada. Canada Dept. For., For. Entomol. and Pathol. Br., Bi-Monthly Prog. Rept. 21 (4): 3.
- Zahner, R. and N. V. DeByle 1965. Effect of pruning the parent root on growth of aspen suckers. Ecology 46: 373-375.
-
- and J. R. Donnelly 1967. Refining correlations of water deficits and radial growth in young red pine. Ecology 48: 525-530.

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MOSQUITO STUDIES (Diptera, Culicidae)

XIII. PUPAE OF THE GENUS PSOROPHORA IN
NORTH AMERICA AND PUERTO RICO¹

By

A. Ralph Barr²

and

Sylvia Barr

Fourteen species of *Psorophora* have been reported from America north of Mexico and Puerto Rico (Carpenter and LaCasse 1955; Stone, Knight and Starcke 1959). It is not possible at the present time to identify pupae in this genus because none has been described in detail. Neither is there a published key by which pupae of this genus may be separated from others occurring in North America. This study contains descriptions of 13 of the 14 species of *Psorophora* known from North America and Puerto Rico and discusses their identification. A generic diagnosis and discussion of generic classification is also included.

This study was made possible by the loan or donation of specimens by the following individuals: Harry D. Pratt, Alan Stone, John N. Belkin, James S. Haeger and Nina Branch, Osmun P. Breland, R.E. Bellamy, W.R. Horsfall, William Wills, and Harold C. Chapman. To all of these individuals the authors are deeply grateful.

MATERIALS AND METHODS

Pupal exuviae were mounted as described by Barr (1958). After the specimen was dissected and positioned in a small amount of thin Canada balsam, a large coverslip was placed on the exuviae and gentle but firm pressure applied to flatten the preparation. Specimens were examined with a phase contrast microscope at an appropriate magnification, usually 128 diameters, for counting branches of setae. The numbering system used for the abdominal setae was that of Barr and Myers (1962). Cephalothoracic setae were numbered in the conventional manner as illustrated in Barr (1963). The "usual" number of branches as used in this study is a restricted range which usually includes 90% or more of the observations; only unusual values

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²School of Public Health, University of California, Los Angeles, California 90024.

are excluded. The widths of respiratory trumpets as given must be interpreted with care as they vary with mounting method and are not strictly comparable in various kinds of mounts.

Genus *Psorophora* Robineau-Desvoidy, 1827

PUPA. Very large to small. Cephalothoracic setae more or less normal for the family; 1 long; 2 usually shorter than 3; 4 and 5 well developed and subequal; 7 much longer than 6; 8 and 9 usually well developed and well separated. Respiratory trumpet about 1-1/2 to 4 times as long as its pinna. Abdomen usually without reticulation between float hairs (1) on I; float hairs usually with small number of stalks at base; 2 usually medial of 4 on I; I-6 and I-7 subequal in length, both usually branched; I-9 commonly branched; venter of I commonly with a seta. Seta 5 usually longer than, and medial of, 3 on II; 6 and 7 usually subequal in length and branched on II; venter of II commonly with a "transitory" seta. Seta 5 usually longer than, and medial of, 3 on III. Setae 1 and 5 usually well developed and subequal in length on IV and V; 4 usually longer than, and medial of, 3 on these segments. Seta 3 medial of, and occasionally longer than, 1 on VI; both usually much shorter than VI-5. Seta 6 usually smaller than, and anterior and medial of, 9 on VII. Segment VIII usually with conspicuous extensions (lobes) of the sternum and tergum which partially cover the bases of the paddles (fig.1a); seta 9 inserted on the venter slightly before the posterior corner, occasionally on the margin. IX without a seta. Paddles pear-shaped, with conspicuous midrib not reaching margin; usually without strong denticulation; accessory seta present or absent; paddle seta commonly branched.

There appears to be no single character by which the genus may be defined. The conspicuous flaps on VIII (fig.1a) have not been seen by the writers in pupae of other genera but, unfortunately, are not well developed in the subgenus *Grabhamia* (fig.2a). The position of 6 on VII (anterior of 9) is unusual although not invariable in the genus. The placement of 3, medial of 1, on VI is unusual but not unique to the genus. Another difficulty with this character is that 3 and 1 are not always readily distinguishable. If 1 is much larger than, but lateral of 3, as is usually the case, the reversal is quickly noted. If, on the other hand, 3 is as large as or larger than 1, the reversal is not apparent. These setae seem always to be reversed in *Psorophora* pupae, however, as shown by an examination of the prepupa or larva (Barr and Myers 1962) in doubtful cases. The reduction in the seta which is apparently VI-1 (actually 1 or 3) as compared with 5 is characteristic of the genus. The reduction in size of the dorsal setae on VII is also characteristic of, although not unique to, the genus.

Psorophora pupae are most likely to be confused with those of *Culiseta* or *Aedes*. Pupae of *Psorophora* have either: (1) large spines in the posterior corner of segment IV (fig.6), (2) an accessory paddle seta, or (3) prominent lobes on the posterior margins of segment VIII. These characteristics do not occur in *Aedes* or *Culiseta* pupae except that an occasional species, as *Culiseta melanura* (Coquillett) or *Aedes atropalpus* (Coquillett), may have an accessory paddle seta. The following key will aid in separating these groups.

KEY FOR SEPARATION OF PUPAE OF *PSOROPHORA*, *CULISETA*, AND *AEDES*

1. Posterior corner of segment IV with large spines (fig.9).

- *Psorophora (Janthinosoma) part*
 Posterior corner of segment IV without large spines. 2
2. Posterior margin of sternum VIII with conspicuous lobes 3
 Posterior margin of sternum VIII without conspicuous lobes 4
3. Accessory paddle seta present *Psorophora (Psorophora)*
 Accessory paddle seta absent *Psorophora (Janthinosoma) part*
4. Accessory paddle seta present 5
 Accessory paddle seta absent 6
5. Either respiratory trumpet split almost completely to base, or paddle margin
 with large, needle-like denticles, or paddle deeply incised; 9 anterior of 6 on
 VII 6
 Respiratory trumpet not split almost completely to base; paddle margin with-
 out large, needle-like denticles; paddle not deeply incised; 9 usually not an-
 terior of 6 on VII. *Psorophora (Grabhamia)*
6. Setae 1 and 5 subequal in length on IV to VI or paddle margin with long,
 needle-like denticles; with seta on IX; with prominent spines on hypopygium
 *Culiseta*
 Seta 5 usually much longer than 1 on IV to VI; paddle margin usually without
 long, needle-like denticles; usually without seta on IX; usually without prom-
 inent spines on hypopygium. *Aedes*

KEY TO NORTH AMERICAN PSOROPHORA PUPAE

1. Posterior corners of IV with large spines (fig.9); accessory paddle seta usually
 absent (*Janthinosoma*, except *cyanescens*) 2
 Posterior corners of IV without large spines ventrally; accessory paddle seta
 usually present (except *cyanescens*), sometimes indistinct 6
2. CT-10 usually with 3 or fewer branches; II-5 usually with 4 or fewer branches;
 III-1 usually with 6 or fewer branches; III-5 usually with 4 or fewer branches
 *varipes*
 CT-10 usually with 5 or more branches; II-5 usually with 5 or more branches;
 III-1 usually with 7 or more branches; III-5 usually with 6 or more branches
 3
3. Heavily pigmented, grossly appears brown, not yellow; respiratory trumpets less
 than 3 times as long as wide; CT-12 usually with 5 or more branches; VII-1
 frequently with 3 or more branches *johnstonii*
 Lightly pigmented, grossly appears yellow; respiratory trumpet 3 or more times
 as long as wide; CT-12 usually with 4 or fewer branches (except *horrida*);
 VII-1 single or double 4
4. II-1 usually with 5 or fewer branches; I-2 usually single; V-8 usually double or
 single; VI-11 usually single; male terminalia as in fig.6 *longipalpus*

- II-1 usually with 7 or more branches; I-2 usually with 2 or more branches; V-8 usually with 3 or more branches; VI-11 usually branched; male terminalia as in fig.5 5
5. CT-12 usually with 2 or fewer branches; I-4 usually with 4 or fewer branches; II-4 usually with 3 or fewer branches *ferox*
 CT-12 usually with 4 or more branches; I-4 usually with 5 or more branches; II-4 usually with 4 or more branches *horrida*
6. Pupa very large; segment III as in fig.1, 4 usually closer to 5 than to 1, usually anterior of and subequal to 5 in length; II-5 and III-5 usually with 3 or fewer branches; VIII-9 usually with 5 or fewer principal branches; CT-10 usually with 4 or fewer branches; CT-8 usually single (*Psorophora*) 7
 Pupa usually medium to small; segment III as in fig.2, 4 usually closer to 1 than to 5, usually posterior of and much longer than 5; II-5 and III-5 usually with 4 or more branches; VIII-9 usually with 6 or more principal branches; CT-10 usually with 5 or more branches; CT-8 usually with 2 or more branches . . 8
7. Segment VIII with dark spots anteriorly and posteriorly on either side of medial line, entire segment usually spotted; without dark medial stripe on abdomen; with diagonal stripes enclosing conspicuous light areas laterally on V to VII (fig.4) *howardii*
 Segment VIII without such dark spots anteriorly and posteriorly although usually with darker medial stripe, segment usually rather evenly dark laterally and on mid-line, with light pigmentation elsewhere; with dark medial stripe on abdomen; without pattern as described above although with diagonal stripes laterally on segments V to VII (fig.3) *ciliata*
8. Accessory paddle seta usually absent; CT-11 usually with 3 or more branches; I-4 usually with 6 or more branches; II-4 usually with 4 or more branches; III-4 usually with 4 or more branches *cyanescens*
 Accessory paddle seta usually present; CT-11 usually single, occasionally double; I-4 usually with 4 or fewer branches; II-4 usually with 3 or fewer branches; III-4 usually single or double (*Grabhamia*) 9
9. VII-6 with 4 or fewer branches, usually double or triple; respiratory trumpet usually 2 or fewer times as long as its pinna; I-3 usually with 10 or fewer branches; V-3 with 5 or fewer branches *insularia*
 VII-6 with 6 or more branches; respiratory trumpet usually over twice as long as its pinna; I-3 usually with more than 10 branches; V-3 usually with 6 or more branches 10
10. I-5 with 4 or fewer branches; I-7 with 5 or more branches; III-6 with 3 or more branches; IV-1 with 4 or more branches; IV-6 with 3 or more branches; V-1 usually branched; V-8 with 4 or more branches; VI-6 frequently with 3 or more branches; VII-5 with 3 or more branches *pygmaea*
 I-5 with 5 or more branches; I-7 usually with 4 or fewer branches; III-6 usually double or single; IV-1 double or single; IV-6 double or single; V-1 usually single (except *discolor*); V-8 usually with 3 or fewer branches; VI-6 single or double; VII-5 usually double or single 11

11. I-4 with 4 or more branches; VII-3 usually with 4 or more branches
 *signipennis*
 I-4 single or double; VII-3 usually with 3 or fewer branches. 12
12. Paddle seta very long, about 1/4 or more the length of the paddle (fig.8); VII-1
 usually placed about midway between lateral edge of segment and mid-line
 *discolor*
 Paddle seta of normal length, usually less than 1/6 the length of the paddle;
 VII-1 usually much closer to mid-line than to lateral edge of segment (fig.2)
 *confinnis*

Subgenus *Psorophora* Robineau-Desvoidy, 1827

PUPA. Very large; with conspicuous dark areas, either in lines (*ciliata*) or spots (*howardii*), on various parts of the abdomen; bases of major setae usually surrounded by dark spots; setation generally short in comparison with that of the other subgenera. CT-8 usually single; CT-10 usually with 4 or fewer branches; respiratory trumpet usually less than twice as long as its pinna. II-5 usually with 3 or fewer branches. Seta 4 removed laterally, and similar to 5, on II and III; usually it is at least as close to 5 as to 1 and only slightly, if at all, posterior of 5. Usually with a "transitory" seta or at least a conspicuous sensillum on the venter of II. III-1 usually with 4 or fewer branches; III-5 usually with 3 or fewer branches. VI-3 usually smaller than VI-1 and both conspicuously smaller than VI-5. Segment VIII with conspicuous lobes on posterior margin of sternum; VIII-9 usually with 5 or fewer branches. Accessory paddle seta present although frequently indistinct; paddle usually obliquely truncate and about as wide as long.

Pupae of the subgenus *Psorophora* can usually be easily recognized by their large size, extensive pigmentation, wide paddles, presence of accessory paddle seta, presence of lobes on sternum VIII, and pattern of setation on II and III.

Psorophora (*Psorophora*) *ciliata* (Fabricius, 1794)

PUPA. Not previously described in its entirety. Partial descriptions have been given by Mitchell (1907), Howard, Dyar, and Knab (1912, 1917), Knight and Chamberlain (1948), and Lane (1953).

Very large; respiratory trumpet 1.8 to 2.1 times as long as its pinna; occasionally with a ventral seta on I. Venter of II usually with conspicuous sensilla. Paddle about 1.2 to 1.3 times as long as wide, with few, small, rounded denticles. A summary of the setal branchings is given in Table 1.

This pupa is not likely to be confused with others except *howardii*. The abdominal markings have been described by Lane (1953) and, although variable, seem invariably to be reliable for separating this pupa from that of *howardii*. The exuviae of *ciliata* grossly appear to have three longitudinal, dark lines while those of *howardii* have a mottled appearance. CT-6 may also be useful in this separation. *P. howardii* also generally has broader paddles with more and longer denticles than does *ciliata*.

Material examined: 3 specimens from Virginia, 2 from Maryland, and 1 from New York, all in the U.S. National Museum; 19 specimens from St. Paul, Minnesota in the collection of the writers.

Psorophora (Psorophora) howardii Coquillett, 1901

PUPA. Not previously described in its entirety although partial descriptions are given by Mitchell (1907) and Lane (1953). The abdominal markings have been described by Lane (1953).

Large to very large; abdomen conspicuously spotted; respiratory trumpet 1.7 to 2.0 times as long as its pinna; usually with a ventral seta on I; usually with a "transitory" seta on the venter of II; paddle 1.0 to 1.1 times as long as wide, with moderate number of small to medium, rounded denticles. A summary of the setal branchings is given in Table 1.

Material examined: 5 specimens from Louisiana, 1 each from Arkansas and Missouri, 2 from Mexico, 1 from Nicaragua, and 1 without data, all in the U.S. National Museum. Also 16 specimens from Florida in the collection of the writers, supplied by J.S. Haeger and Nina Branch.

Subgenus Janthinosoma Lynch Arribalzaga, 1891

PUPA. Usually medium or small; CT-8 usually branched; CT-10 usually with 5 or more branches (except *varipes*); respiratory trumpet about 2 to 4 times as long as its pinna. II-5 usually with 4 or more branches. Seta 4 closer to 1 than to 5 on III and frequently on II, usually markedly longer and much posterior of 5. III-1 usually with 5 or more (except *cyanescens*) and III-5 usually with 4 or more (except *varipes*) branches. All species except *cyanescens* have a patch of large, cuticular spines in the posterior corner of IV. On VI seta 3 may be larger or smaller than 1. Segment VIII with conspicuous lobes on posterior margin of sternum; VIII-9 usually with 6 or more branches. Accessory paddle seta absent. Paddle with weak denticulation.

Janthinosoma pupae (except *cyanescens*) may be easily recognized by the large spines on IV; these do not occur in other subgenera. The subgenus is also distinguished by lacking an accessory paddle seta although it occasionally occurs as an anomaly in at least *johnstonii* and *varipes*.

Psorophora (Janthinosoma) cyanescens (Coquillett, 1902)

PUPA. Previously undescribed. Medium to large; respiratory trumpet 1.7 to 2.6 times as long as its pinna; frequently with a ventral seta on I; occasionally with a "transitory" seta on II. A summary of the setal branchings is given in Table 1.

The pupa of this species has II-4 more highly branched than in other *Psorophora* species. It can be separated from *Grabhamia* and *Psorophora* by lacking the accessory paddle seta and from other *Janthinosomas* by lacking the prominent spines on IV.

Material examined: 10 specimens from Wilson Dam, Alabama, in the collection of J.N. Belkin (UCLA); and 11 specimens from Cameron, Louisiana, in the collection of the writers, supplied by H.C. Chapman.

Psorophora (Janthinosoma) ferox (Humboldt, 1819)

PUPA. Partially described by Mitchell (1907), Howard, Dyar, and Knab (as *sayi*; 1912, 1917) and Lane (1953).

Medium to large; respiratory trumpet 3.0 to 4.3 times as long as its pinna; frequently with a ventral seta on I; paddle with sparse, weak denticles. A summary of the setal branchings is given in Table 1.

The presence of large spines on IV marks this species as a typical *Janthinosoma*, and allies it with *horrida*, *longipalpus*, *johnstonii*, and *varipes*. It is generally markedly larger than the other four species; it also has longer respiratory trumpets and less pigmentation than *johnstonii*. The key characters given should allow the separation from *varipes* without difficulty. The pupa of *ferox* is most likely to be confused with those of *longipalpus* and especially *horrida*; the key as given serves fairly well for the specimens at hand but may require modification when additional material is examined.

Material examined: 2 specimens from Piraja, Brazil in the collection of the U.S. National Museum; 1 specimen without data in the collection of R.E. Bellamy; 9 specimens from Wilson Dam, Alabama, in the collection of J.N. Belkin (UCLA); and 4 specimens from Lufkin, Texas, collected by O.P. Breland and 26 specimens from Florida, collected by J.S. Haeger, in the collection of the writers.

Psorophora (Janthinosoma) horrida (Dyar and Knab, 1908)

PUPA. Previously undescribed; small to medium; respiratory trumpet 3.0 to 3.7 times as long as its pinna; no ventral seta on I or II in the specimens examined. Paddles with sparse, weak denticulation. A summary of the setal branchings is given in Table 1.

This pupa has CT-12, I-9, II-4, III-4, III-10, VI-4 and VI-8 uncommonly highly branched. The description is based on 15 entire pupae from Illinois reared by W.R. Horsfall. Additional characteristics may become evident when exuviae are examined.

Psorophora (Janthinosoma) longipalpus Randolph and O'Neill, 1944

PUPA. Previously undescribed; small to medium; respiratory trumpet 3.0 to 3.8 times as long as its pinna; frequently with a ventral seta on I; venter of II usually without a "transitory" seta; paddle with few, small denticles. A summary of the setal branchings is given in Table 1.

CT-10 and II-1 have fewer branches than in most species. The pupa is most likely to be confused with those of *horrida* and *ferox*. The bulbous terminalia of the male are evidenced in the pupa by the very wide basimeres.

Material examined: 12 specimens from Douglas County, Kansas, in the collection of the writers.

Psorophora (Janthinosoma) johnstonii (Grabham, 1905)

PUPA. Partially described by Thurman, Haeger, and Mulrennan (1951) and Lane (1953).

Small; with dark, rather uniform pigmentation; respiratory trumpet 2.3 to 2.8 times as long as its pinna; ventral seta frequently present on I; II frequently with "transitory" seta; paddle with very few, small denticles; accessory paddle seta occasionally present. A summary of the setal branchings is given in Table 1.

The pupa of this species is a small, dark *Janthinosoma* with short respiratory trumpets. It has CT-12 uncommonly highly branched for this group.

Material examined: 12 specimens from Florida collected by J.S. Haeger in the collection of the writers.

***Psorophora (Janthinosoma) varipes* (Coquillett, 1904)**

PUPA. Partially described by Mitchell (1907).

Small; respiratory trumpet 2.1 to 3.9 times as long as its pinna; usually with ventral seta on I and "transitory" seta on II; paddle with medium to large denticles; accessory paddle seta occasionally present. A summary of the setal branchings is shown in Table 1.

This is a small *Janthinosoma* pupa with generally reduced setal branchings. It can be distinguished from related forms especially in the reduced branching of CT-10, I-3, I-4, I-5, II-5, III-5, V-7, and VI-6.

Material examined: 16 specimens from Wilson Dam, Alabama, in the collection of J.N. Belkin (UCLA); 1 specimen from Georgia in the collection of R.E. Bellamy.

Subgenus *Grabhamia* Theobald, 1903

PUPA. Usually medium to small; CT-8 usually branched; CT-10 usually with 5 or more branches; respiratory trumpet about 1-1/2 to 3 times as long as its pinna. II-5 usually with 4 or more branches. Seta 4 usually closer to 1 than to 5 on III and frequently on II, usually markedly longer and much posterior of 5. III-1 usually with 5 or more and III-5 with 4 or more branches. Seta 1 is usually larger than 3 on VI. Segment VIII without conspicuous lobes on posterior margin of sternum; VIII-9 with 6 or more branches. Accessory paddle seta present. Paddle usually with weak denticulation.

Grabhamia pupae lack the conspicuous lobes on VIII of the other two subgenera, but possess an accessory paddle seta. They are most likely to be confused with *Culiseta* and *Aedes* pupae which, however, generally lack an accessory paddle seta. In addition, *Grabhamias* lack the seta on IX found in *Culiseta* and occasionally in *Aedes*. The position of 6 with respect to 9 on VII is also useful in distinguishing *Grabhamia* pupae from those of *Aedes* and *Culiseta*.

***Psorophora (Grabhamia) confinnis* (Lynch Arribalzaga, 1891)**

PUPA. Partially described by Mitchell (1907), Howard, Dyar, and Knab (as *columbiae*; 1912, 1917), and Lane (1953).

Medium to large; respiratory trumpet 1.9 to 2.8 times as long as its pinna; frequently with ventral seta on I; II occasionally with "transitory" seta; paddle with few, small denticles. A summary of the setal branchings is given in Table 1.

The pupa of this species is characterized by lacking characteristics of other *Grabhamia* pupae. Two specimens from the Virgin Islands were excluded because of the highly branched nature of CT-4, 10, 11, seta 6 on I to III and VI, IV-1, and VII-5. It is problematic whether these specimens are conspecific with the others. Three specimens from Brazil and two from Mexico agreed reasonably well with material

from the United States.

Material examined: 3 specimens from Porto Alegre, Brazil; 2 specimens from Salina Cruz, Mexico; 3 specimens from Arkansas, 2 from Louisiana, 3 from Virginia, 2 from St. Croix, Virgin Islands, and 4 without data, all in the U.S. National Museum. Also 16 specimens from Florida, collected by J.S. Haeger, and 25 from Thermal, California, collected by William Wills in the collection of the writers.

Psorophora (Grabhamia) discolor (Coquillett, 1930)

PUPA. Partially described by Mitchell (1907).

Medium size; respiratory trumpet about twice as long as its pinna; frequently with ventral seta on I; occasionally with "transitory" seta on II; paddle with few, small denticles. A summary of the setal branchings is given in Table 1.

The pupa of this species may be distinguished from those of all others in the genus by the extremely long paddle seta which is generally more than 1/4 the length of the paddle; in related species it is generally less than 1/6 the length of the paddle. In addition, setae 1 are frequently displaced laterally on V and VII. The exceptionally long paddle seta was noted by Mitchell (1907).

Material examined: 6 specimens from Eagletown, Oklahoma, and 1 without data in the collection of the U.S. National Museum; 13 specimens from Wilson Dam, Alabama, and one from Pickwick Lake, Mississippi, in the collection of J.N. Belkin (UCLA); and 3 specimens from Johnson County, Kansas, in the collection of the writers.

Psorophora (Grabhamia) signipennis (Coquillett, 1904)

PUPA. Paddle and trumpet figured by Yamaguti and LaCasse (1951).

Medium size; respiratory trumpet 1.5 to 1.7 times as long as its pinna; without a ventral seta on I or a "transitory" seta on II. Paddle with sparse, small denticles. A summary of the setal branchings is given in Table 1.

The pupa of this species is similar to most *Grabhamia* pupae except for I-4 which is exceptionally highly branched.

Material examined: 24 specimens from Poplar, Montana, in the U.S. National Museum, and 1 from Johnson County, Kansas, in the collection of the writers.

Psorophora (Grabhamia) insularia (Dyar and Knab, 1906)

PUPA. Previously undescribed; small; respiratory trumpet 1.3 to 1.9 times as long as its pinna; 2 usually lateral of 4 on I; often with a ventral seta on I and occasionally with a "transitory" seta on II; denticles on paddle medium to large, sparse to abundant. A summary of the setal branchings is given in Table 1.

This very distinct short-trumpeted pupa is characterized also by usually having 2 lateral of 4 on I, by the denticulation of the paddle, and by the small number of branches in VII-6 and I-3.

The description is based on 3 exuviae, all male, from Losey Field, Puerto Rico, December 1, 1942, in the collection of H.D. Pratt, and 3 pupae, all female, from Mona Island, Puerto Rico, collected by J. Maldonado, April 16, 1954, in the collection of the U.S. National Museum. The material from Losey Field had been identified as *pygmaea* but differed conspicuously from other material identified as that species from Cataño (see *pygmaea*). The identification as *insularia* was by comparison with Maldonado's material supplied by Alan Stone. The two lots of *insularia* also have many differences although both are clearly different from *pygmaea*; the Mona Island material has more branching in CT-6 and 9, I-5 and 6, II-4 and 6, III-4 and 8, IV-3, VII-8 and 11, and VIII-14 than does the Losey Field material. It also has longer trumpets, much less prominent denticulation and only occasionally has 2 lateral of 4 on I. It remains to be seen whether or not these two types of *insularia* are conspecific; for the present the similarities of the two justify their being considered conspecific.

Psorophora (Grabhamia) pygmaea (Theobald, 1903)

PUPA. Previously undescribed; small; respiratory trumpet 2.6 to 3.1 times as long as its pinna; usually with a ventral seta on I and occasionally with a "transitory" seta on II; paddle with small denticles laterally. A summary of the setal branchings is given in Table 1.

This pupa can be distinguished from other *Grabhamia* pupae (except *insularia*) by the small number of branches in I-5 and the large number in IV-1.

Material examined: 2 ♂♂ and 2 ♀♀ from Cataño, Puerto Rico, May 7, 1943, in the collection of H.D. Pratt.

REFERENCES CITED

Barr, A.R.

1958. The mosquitoes of Minnesota (Diptera: Culicidae: Culicinae). Minn. Univ. Agr. Exp. Sta., Tech. Bull. 228. 154 p.

1963. Pupae of the genus *Culiseta* Felt. II. Descriptions and a key to the North American species (Diptera: Culicidae). Entomol. Soc. Amer., Ann. 56:324-330.

Barr, A.R. and C.M. Myers

1962. Pupae of the genus *Culiseta* Felt. I. The homology of larval and pupal setae (Diptera: Culicidae). Entomol. Soc. Amer., Ann. 55:94-98.

Carpenter, S.J. and W.J. LaCasse

1955. Mosquitoes of North America (north of Mexico). Berkeley and Los Angeles, Univ. Calif. Press. 360 p.

Howard, L.O., H.G. Dyar and F. Knab

1912(1913). The mosquitoes of North and Central America and the West Indies. Volume II. Plates. Wash., Carnegie Inst. 150 pl. (Publication 159).

1917. The mosquitoes of North and Central America and the West Indies. Volume IV. Systematic description. Part II. Wash., Carnegie Inst. p.525-1064 (Publication 159).

Knight, K.L. and R.W. Chamberlain

1948. A new nomenclature for the chaetotaxy of the mosquito pupa, based on a comparative study of the genera (Diptera: Culicidae). Helminthol. Soc. Wash., Proc. 15:1-18.

Lane, J.

1953. Neotropical Culicidae. Vol. II. Sao Paulo, Univ. Sao Paulo. p.553-1112.

Mitchell, E.G.

1907. Mosquito Life. New York, Putnam. 281 p.

Stone, A., K.L. Knight and H. Starcke

1959. A synoptic catalog of the mosquitoes of the world (Diptera, Culicidae). Wash., Entomol. Soc. Amer. (Thomas Say Found. Publication 6). 358 p.

Thurman, E.B., J.S. Haeger and J.A. Mulrennan

1951. The taxonomy and biology of *Psorophora (Janthinosoma) johnstonii* (Graham, 1905) (Diptera: Culicidae). Entomol. Soc. Amer., Ann. 44:144-157.

Yamaguti, S. and W.J. LaCasse

1951. Mosquito fauna of North America. Part III. Genera *Orthopodomyia*, *Mansonia*, and *Psorophora*. Kyoto, Honshu, Japan Logistical Command, Office Surg. 92 p.

Table 1. Usual number of branches in setae useful for identifying Psorophora pupae.

<i>(Psorophora)</i>			<i>(Grabhamia)</i>					<i>(Janthinosoma)</i>						
<i>ciliata howardii confinnis discolor pennis pygmaea insularia cyanescens ferox horrida palpus stonii varipes</i>			<i>signi-</i>					<i>longi- john-</i>						
CT	- 1	1-3	1-2	1	1-2	2	1-2	2-3	2	2	2-3	2	2-3	1-2
- 4	1-3	2-3	2-4	2-4	3-6	3-6	4-6	3-5	3-5	2-5	3-6	3-5	3-7	2-4
- 5	1-4	2-4	3-5	3-4	4-6	4-6	4-7	3-5	2-6	2-3	2-4	2-4	3-6	2-3
- 6	3-5	1-2	3-5	3-6	2-4	2-4	3-5	3-5	2-5	2-4	2-4	2	1-3	1-2
- 8	1	1	1-3	2-3	2-4	2-4	2-3	3-5	3-5	2-6	3-5	2-4	3-5	1-2
-10	1-4	2-5	4-13	5-14	9-21	10-19	9-14	4-12	5-10	4-7	4-7	4-7	7-9	2-3
-11	1-2	1-2	1	1	1-2	1-2	1-3	2-4	1-3	2-3	2-3	2-3	1-2	1-2
-12	2-3	1-4	1-2	2-3	3-6	2-5	3-4	3-4	2	4-8	2-4	2-4	4-9	2-3
I	- 2	1-2	1	1-4	1-4	1	1-2	2-4	1-4	2-4	2-4	1-2	1-3	1-2
- 3	8-18	6-9	13-26	10-23	12-18	12-15	7-10	11-22	11-16	16-23	12-18	14-20	7-11	
- 4	3-6	2-3	1-2	1-2	4-5	1-2	2-4	5-11	2-4	5-8	3-5	3-6	2-3	
- 5	2-6	2-3	6-12	6-11	5-9	3-4	3-8	6-10	5-11	5-9	4-6	5-7	2-5	
- 6	3-5	2-3	2-4	2-4	3-6	4-5	3-7	3-5	2-3	2-4	2-4	3-4	1-2	
- 7	3-9	5-8	2-6	3-4	1-2	5-6	4-5	4-7	2-5	5-7	3-5	4-8	2-4	
- 9	1-4	1-2	1-4	1-3	3-7	1	1-2	1-4	1-3	3-5	1-2	1-2	1-2	
II	- 1	3-10	4-8	5-13	10-15	4-11	9-16	8-18	7-13	7-14	3-5	3-9	9-14	
- 3	5-7	4-8	7-16	6-17	7-10	6-12	5-8	6-9	6-10	4-7	4-7	6-9	3-6	
- 4	1-3	2-3	1	1-2	1-3	1-2	1-4	3-7	2-3	4-8	3-5	2-4	1-4	
- 5	1-4	1-3	4-7	5-7	6-10	5-8	4-7	5-9	5-7	5-8	5-8	5-8	2-4	

II	- 6	2-5	1-3	2-3	2-4	2-5	4-6	3-10	2-5	2-3	2-4	2-3	2-4	2
	- 7	4-8	3-6	3-7	2-5	4-7	5-8	3-6	4-6	2-5	3-7	3-5	4-7	2-4
III	- 1	3-4	2-3	3-8	4-8	5-11	6-13	4-7	2-5	5-10	6-12	6-10	6-15	3-6
	- 3	2-5	3-5	5-9	6-10	4-9	4-6	4-7	4-8	3-8	4-7	4-7	5-8	3-5
	- 4	2-3	1-3	1-2	1-2	1-3	1-2	1-3	3-5	1-3	3-6	2-3	1-3	1-3
	- 5	1-3	1-3	4-7	6-11	8-13	4-9	4-7	5-9	6-9	6-13	6-10	5-8	2-4
	- 6	2-6	1-3	1-2	1-2	1-3	3-4	2-4	2	2-3	2	1-2	2-3	1-2
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	- 7	5-7	5-8	4-9	4-7	3-5	3-5	2-6	4-8	3-5	3-6	3-5	4-6	2-4
	- 8	2-3	1-3	2-5	2-5	2-3	3-4	3-5	4-7	2-4	2-3	1-2	2-4	2-4
	-10	2-3	2-3	1-2	1	1-2	1-2	1-2	2-4	2	2-3	2-4	1-3	1-2
	-11	3-5	1-4	1-2	1-2	1	1-3	2-4	1-2	1-2	2-3	1	1	1
V	- 1	2	1-3	1	1-3	1	2-3	2-4	2	2	2	2	2-3	1-2
	- 3	4-10	4-8	5-9	6-9	6-12	5-9	3-5	5-10	6-9	7-11	5-7	6-10	5-6
	- 4	1-4	2-3	2-4	1-4	3-4	3-4	2-3	4-5	2-3	2-3	2-3	2-3	1-3
	- 6	2-3	1-2	1-2	1-2	1-2	2-4	1-2	1-2	1	1	1-2	1-2	1

Table 1 (cont.)

<i>(Psorophora)</i>				<i>(Grabhamia)</i>				<i>(Janthinosoma)</i>						
	<i>ciliata</i>	<i>howardii</i>	<i>confinnis</i>	<i>discolor</i>	<i>pennisi</i>	<i>pygmaea</i>	<i>insularia</i>	<i>cyanescens</i>	<i>ferox</i>	<i>horrida</i>	<i>palpus</i>	<i>longi-johnstonii</i>	<i>varipes</i>	
- 7	5-10	4-8	5-11	5-9	5-8	4-9	3-5	6-13	6-9	6-11	6-9	7-11	3-6	
- 8	1-3	1-3	2-4	2-4	2-3	4-6	3-4	3-5	3-4	3-5	1-2	2-4	2-3	
-11	4-5	1-4	2-4	1-3	1	1-3	2-3	1-4	1-2	1-2	1	1	1	
VI - 3	3-4	2-4	2-5	1-5	1-2	2-4	2-3	1-6	2-3	2	2	1-3	1-3	
- 4	1-4	2-4	2-4	2-5	3-5	2-5	2-4	4-7	2-4	4-7	3-5	3-5	2-3	
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-11	2-4	1-3	2-5	3-6	2-4	2-5	2-4	2-5	1-3	1-2	1	1	1	
VII - 1	2-3	1-3	1	1-2	1-3	1-2	1-3	1-3	1-2	1-2	1-2	2-4	1-2	
- 3	2-3	1-2	2-3	2-4	3-7	2-5	2-3	3-7	2-4	3-5	3-5	2-5	2-3	
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- 6	5-8	5-8	7-18	8-17	7-17	7-14	2-3	11-27	5-10	9-15	5-8	6-14	3-5	
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- 8	6-12	5-11	3-10	5-10	5-11	3-8	2-5	7-19	3-7	5-10	3-5	4-8	3-4	
- 9	4-7	2-4	4-9	4-7	4-9	4-7	2-5	5-12	2-3	2-4	3-4	2-5	1-3	
-10	1-2	1	1	1	1	1	1	1-3	2	1-3	1-2	1-2	1-2	
-11	1-2	1-2	2-4	2-4	1-3	1-4	1-2	2-4	2-3	2-3	2	1-3	1	
VIII- 9	2-5	3-5	6-10	7-12	7-10	6-9	6-11	6-12	6-9	6-13	6-8	7-10	5-7	

FIGURES

- Fig.1. *Psorophora (P.) howardii*; metanotum and abdomen.
Fig.2. *Psorophora (G.) confinnis*; metanotum and abdomen.
Fig.3. *Psorophora (P.) ciliata*; pigmentation pattern of metanotum and abdomen.
Fig.4. *Psorophora (P.) howardii*; pigmentation pattern of metanotum and abdomen.
Fig.5. *Psorophora (J.) cyanescens*; metanotum and abdomen.
Fig.6. *Psorophora (J.) longipalpus*; metanotum and abdomen.
Fig.7. *Psorophora (J.) cyanescens*; cephalothoracic setae.
Fig.8. *Psorophora (G.) discolor*; paddle.
Fig.9. *Psorophora (J.) longipalpus*; posterior corner of segment IV.
Fig.10. *Psorophora (G.) insularia*; setae of segment I.
Fig.11. *Psorophora (G.) pygmaea*; setae of segment I.

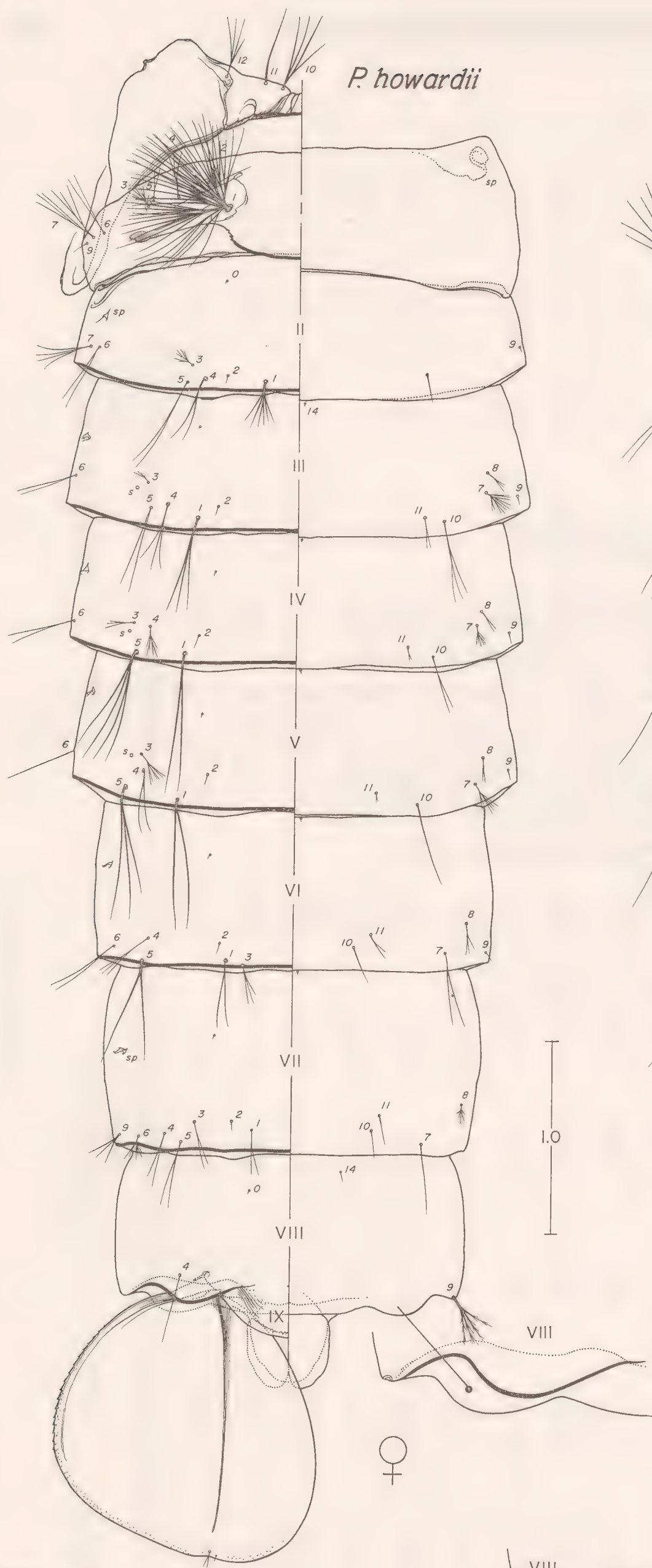


Fig. 1

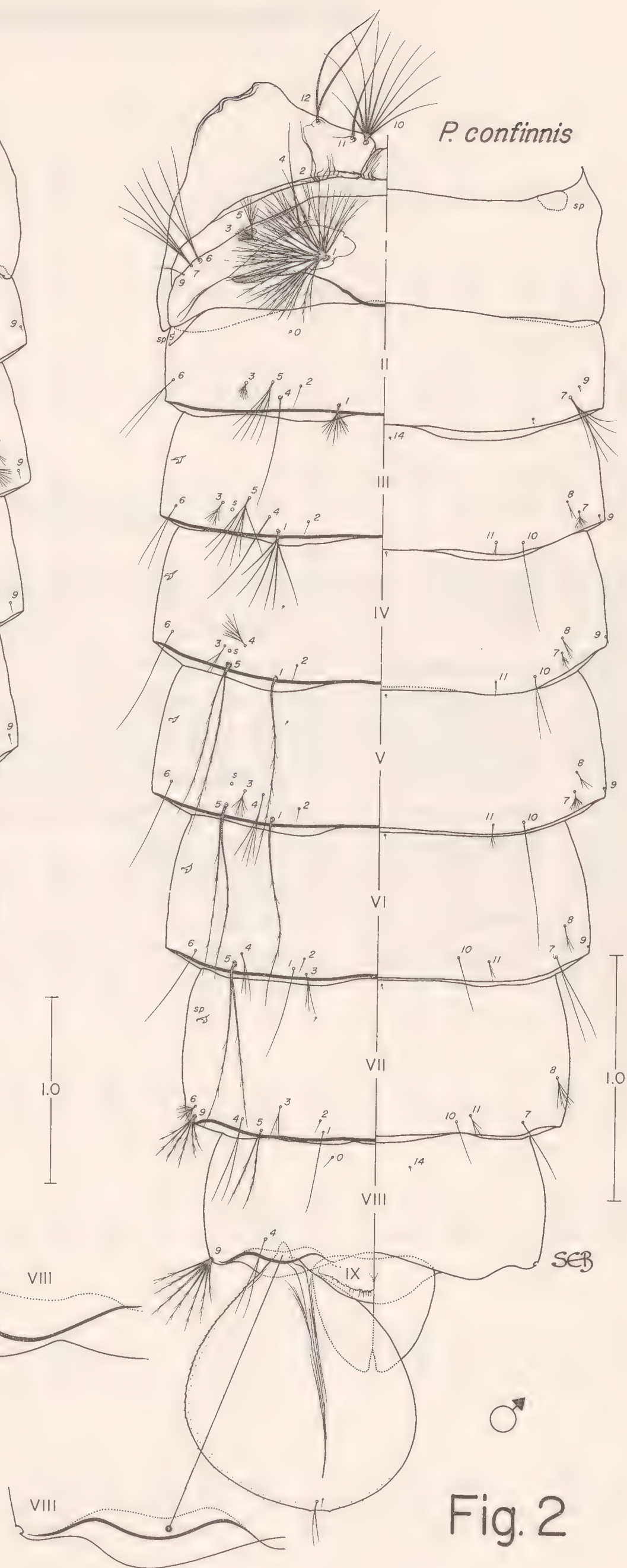


Fig. 2

VIII

Fig. 4

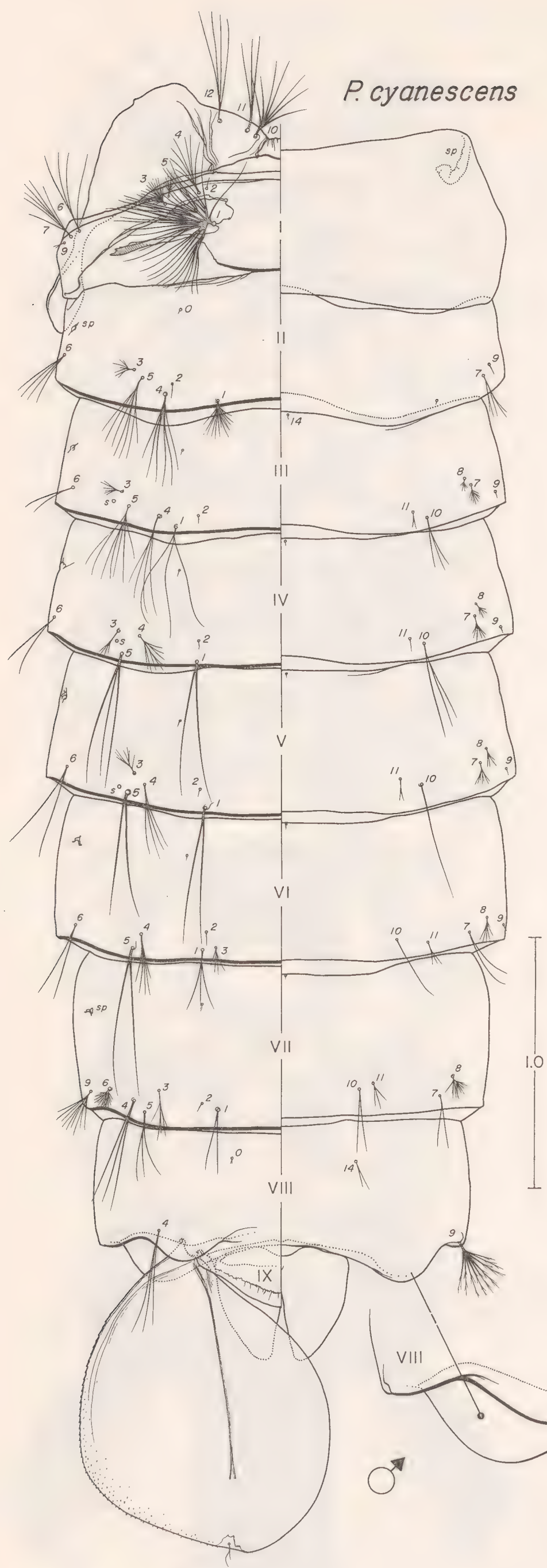


Fig.5

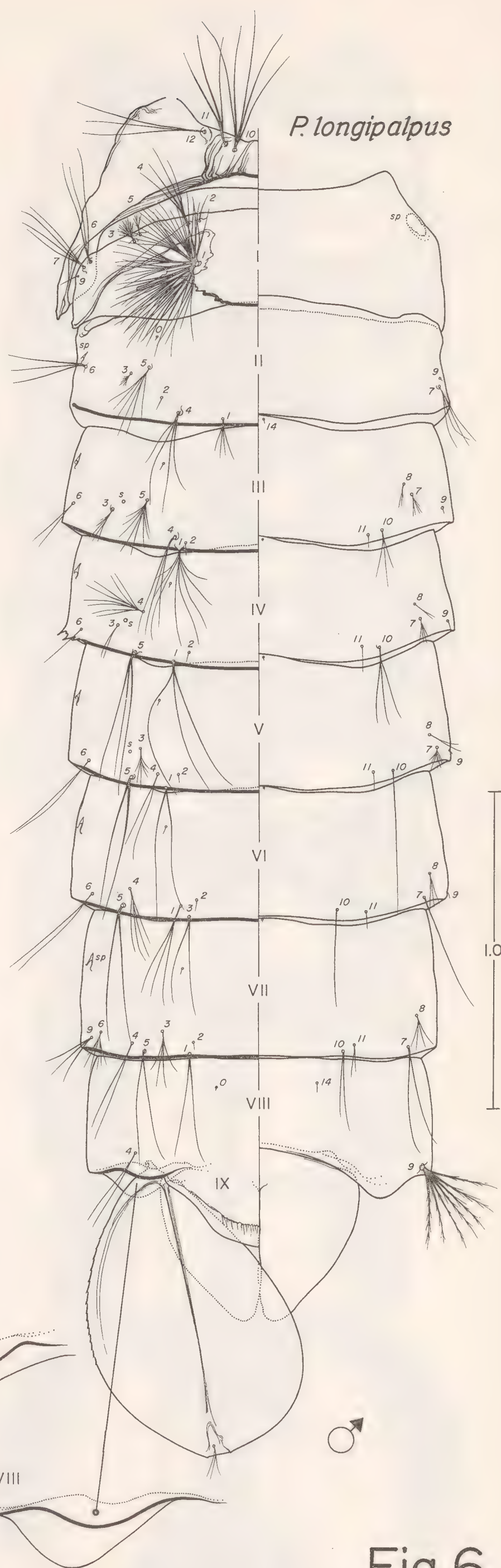
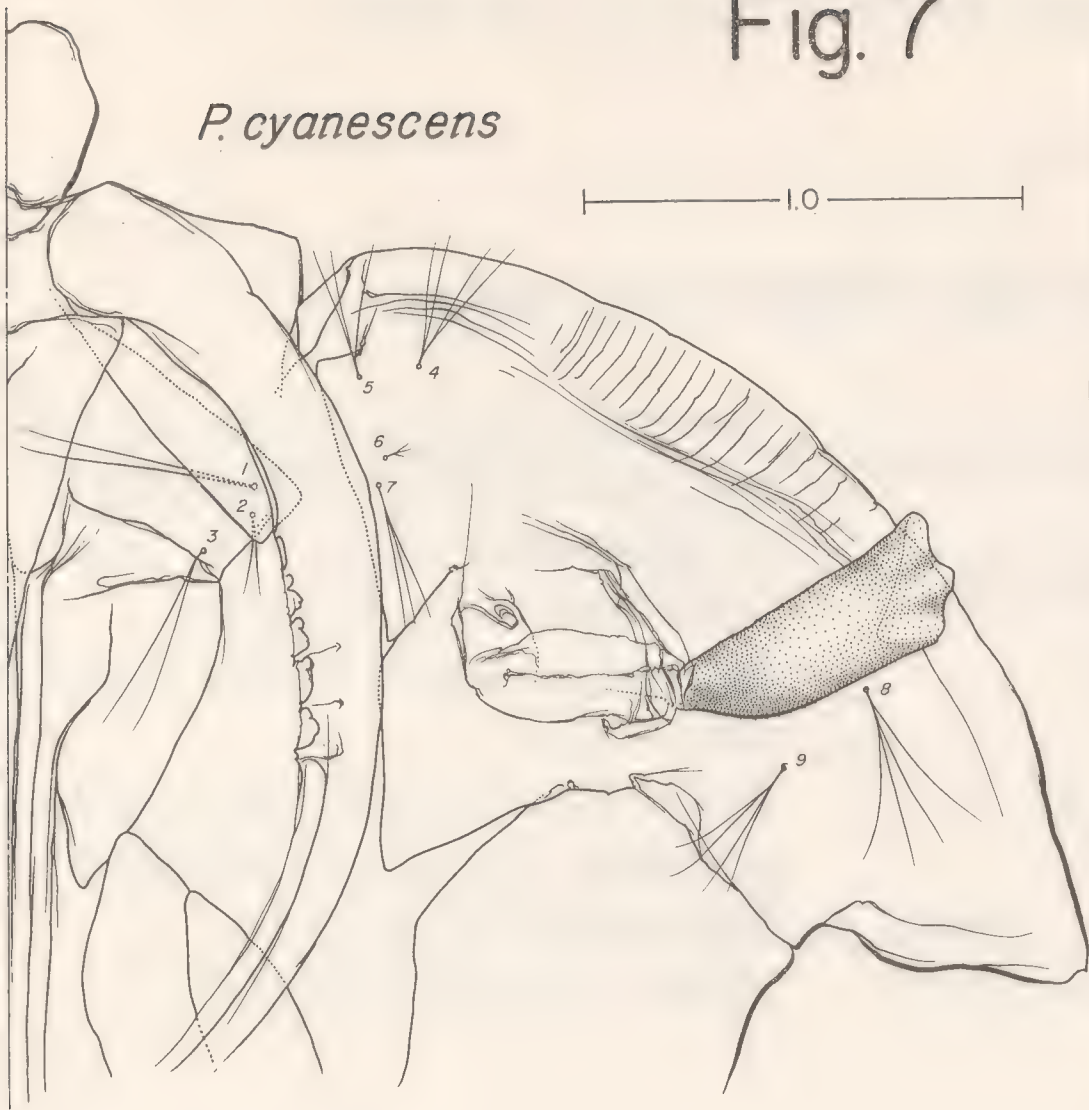


Fig.6

Fig. 7



P. discolor

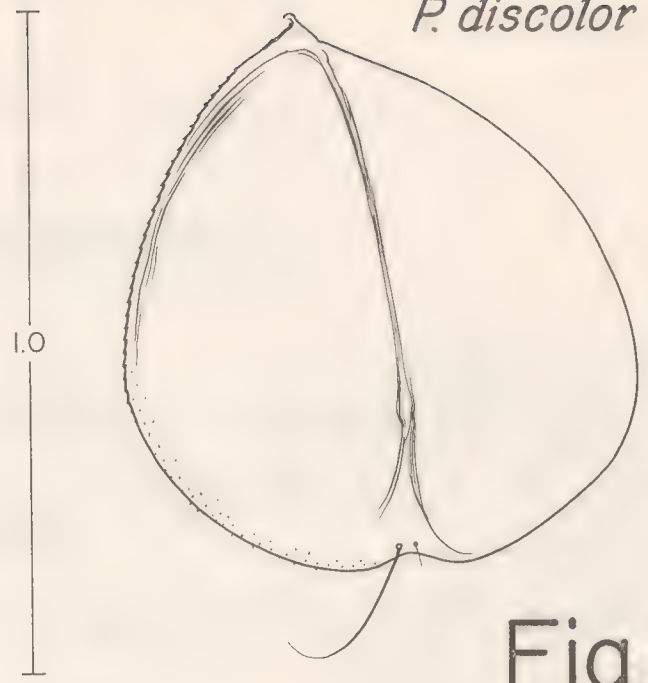
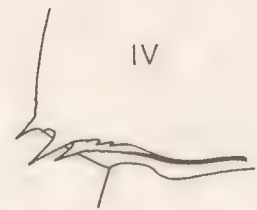


Fig. 8

Fig. 9



1.0

P. insularia

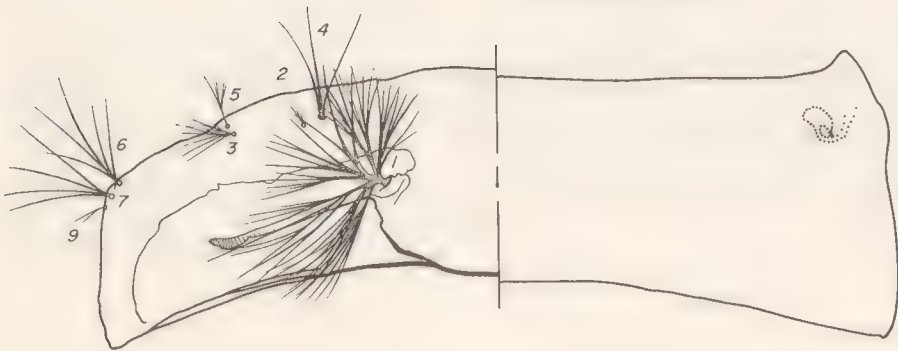


Fig. 10

P. pygmaea

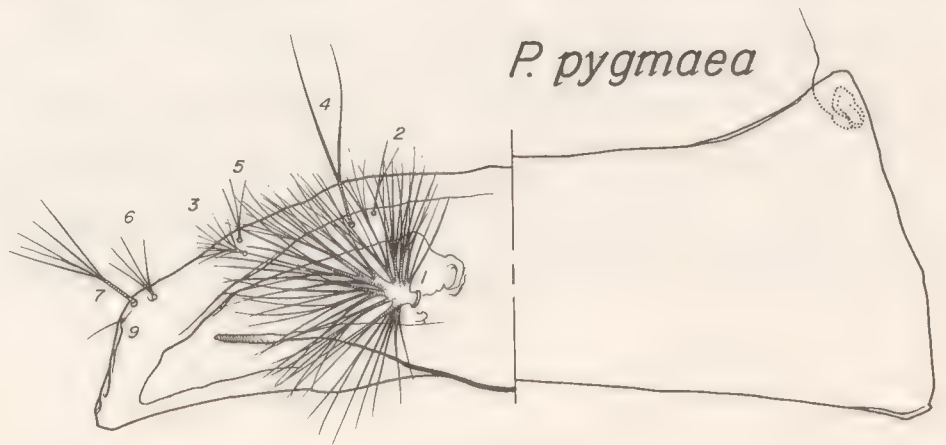


Fig. 11

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MOSQUITO STUDIES (Diptera, Culicidae)

XIV. REDESCRIPTION OF TOXORHYNCHITES (T.) GIGANTULUS FROM THE PHILIPPINES

By

O.G.W. Berlin¹

T. gigantulus has been known only by the holotype ♂ from Limay, Bataan Province, and another ♂ from San Andales, Rizal Province, both collected by R.C. McGregor (USNM). In August 1965 I reared individually 3 larvae and 3 pupae of this species from material brought to our laboratory from the Philippines by Col. Kremmers of the 5th Epidemiological Flight (PACAF), U.S. Air Force. It is now possible to describe all the stages of *gigantulus*. The terminology used in general follows Belkin (1962).

Toxorhynchites (Toxorhynchites) gigantulus (Dyar & Shannon)

Figs. 1, 2

1925. *Megarhinus gigantulus* Dyar and Shannon, 1925:67-68. TYPE: Holotype ♂, Limay, Bataan Province, Luzon, Philippines, Nov 1924, R.C. McGregor [USNM, 28096].

Toxorhynchites (T.) gigantulus of Stone, Knight and Starcke (1959:63).

Megarhinus gigantulus of Edwards (1932:61); Barraud (1934:22); Bohart (1945:23-24); Stone and Knight (1957:200).

FEMALE. Wing: 4.0 mm. Proboscis: 5.0 mm. Forefemur: 3.1 mm. Abdomen: about 4.0 mm. Moderate in size. *Head*: Integument uniformly dark. Scaling on vertex metallic to bluish green, appearing whitish along orbital line. Orbital (2 pairs) and interorbital (1 pair) bristles on dorsal side moderately long. Clypeus dark, with a fine, whitish pubescence. Labial scales purplish. Palpus apparently 4-segmented, about 0.2 of proboscis length; scales as on proboscis. Antenna about 0.5 of proboscis length; torus dark, with a fine, whitish pubescence; flagellar segment 1 with a few dark scales dorsally; flagellar whorls with 6 moderately long bristles, progressively smaller distally. *Thorax*: Integument uniformly black. Mesonotum covered with metallic green scales. Acrostichal, dorsocentral and prescutellar bristles absent; bristles

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on *apn*, anterior promontory, antalar and supraalar areas, *ppl*, upper *pra*, *stp* and upper *mep* distinct. Scales on *apn* bluish green; scales on *ppn* as on mesonotum; *ssp*, *psp* and paratergite bare; *ppl* with silvery scales; *pra*, *stp* and most of *mep* with silvery scales. Scutellum with a continuous row of dark marginal bristles; scales as on mesonotum. *Legs*: Forefemur predominantly dark anteriorly except for basal creamy scales, posterior surface mostly creamy with a few dark scales distally; most of midfemur creamy; hindfemur predominantly creamy on both sides except for dorsal distal dark patch. Tibiae and tarsi of all legs completely dark. *Wing*: Vein scales dark. *Haltere*: Stem pale, knob with creamy scales. *Abdomen*: Laterotergite with median metallic green and lateral creamy scales. Scales on tergites metallic green, to purplish depending on angle of incidence of light. Sternites I-VI completely creamy; distal sternites with basal creamy and apical dark scales. Distinct lateral tufts of long bristlelike scales on segments VI-VIII; apicolateral tuft on VI completely tawny; lateral tuft on VII tawny basally and dark distally; tuft of segment VIII dark.

MALE. *Wing*: 4.0 mm. *Proboscis*: 5.0 mm. *Forefemur*: 3.1 mm. *Abdomen* (including genitalia): about 5.0 mm. Generally similar to female in size and coloration. *Palpus* subequal to proboscis length; 5-segmented, segments 4 and 5 upturned; scaling predominantly purplish except for creamy ventral scales on distal 0.5 of segments 2,3 and proximal 0.5 of 4. *Antenna* about 0.5 of proboscis length; flagellar whorls with 8-10 moderately long bristles, progressively smaller distad. *Legs*: Claws of foreleg and midleg enlarged, unequal; larger claw with a submedian tooth; hindclaws as in female. *Abdomen*: Narrower than in female. Apicolateral tuft on segment VI tawny; lateral tuft on segment VII predominantly tawny with a few dark distal scales; tuft of segment VIII entirely dark.

MALE GENITALIA (fig.1). Ninth tergite lobe shieldlike, with a shallow emargination apically and with about 10 to 12 small to moderately long apicolateral bristles; basal part constricted. Sidepiece about 3.5 as long as its greatest width, with scales ventrally and laterally and bristles on all sides. Clasper (without spiniform) subequal in length to sidepiece; with a small, distinct apical hair, and 2 rows of small setae in distal 0.6; spiniform 0.25 of clasper. Basal mesal lobe with a strong apically curved bristle extending beyond middle of sidepiece and a few smaller subapical bristles of varied length. Aedeagus long, swollen at base and produced distally as a narrow process ending in a recurved tooth; without a narrow submedian dorsal bridge. Paraproct long, slender and strongly sclerotized; cercal setae 3 in number.

PUPA (fig.1). *Abdomen*: 4.6 mm. *Trumpet*: 0.7 mm. *Index* about 3.4-3.7. *Paddle*: 1.35 mm. Chaetotaxy as figured, hairs moderately to darkly pigmented. All normal hairs present. *Cephalothorax*: Moderately pigmented. Middorsal ridge moderate. Hair 1-C strongly developed, single; hairs 2,3-C close together; hairs 6,7-C far forward of 4,5-C; hairs 8,9-C close together and distinctly caudad of trumpet base. *Trumpet*: *Index* about 3.4-3.7; strongly pigmented; pinna moderate. *Metanotum*: Moderately pigmented. Hairs 10,11-C removed from 12-C, moderately close together; an accessory hair caudad of hair 12-C. *Abdomen*: Integument strongly pigmented, progressively lighter on distal segments. Dorsal sensillum on III and IV only. Hair 1-I dendritic; hair 1-III,VII single to triple, short, usually not reaching apex of its tergite; hair 5-III-VI strongly developed, single, extending beyond apex of succeeding segment; hair 6-V,VI strongly developed, single, extending beyond apex of succeeding segment; hair 6 on other segments short to moderately long, barely reaching apex of its tergite; hair 8-VI,VII dorsal, cephalad of 6; hair 9-VIII at caudolateral angle, short to moderately long, single. *Terminal Segments*: Hair 1-IX small, indistinct; hair 1-X distinct and usually 3 branched (1-5). *Paddle*: Relatively broad;

external buttress more or less distinct; margin with distinct hairlike spicules; apex slightly emarginate at level of midrib. Male genital lobe extending to 0.6 and female bare to 0.2 of paddle.

LARVA (fig.2). Head: 1.15 mm. Siphon: 0.6 mm. Anal Saddle: 0.4 mm. Chaetotaxy as figured, hairs moderately to darkly pigmented. In life larvae appear purplish. All normal hairs present. *Head*: Width roughly subequal to length. Mental plate short and very broad, teeth irregular and strongly developed. Hair 4-C mesad of 1; hairs 5-8-C in a row; hairs 11-13-C in lateral cephalic groups; hairs 14,15-C, single, removed cephalad. *Antenna*: Length about 0.25 of head; cylindrical and without spicules; hair 1-A inserted beyond 0.75 from base, branched; hairs 2,3-A basad of 1. *Thorax*: Hairs 1,2-M on a circular tubercle; hairs 3,4-M on an irregular tubercle, separate from hair 6; hairs 5,6,7-M on a larger sclerotized plate. *Abdomen*: Dorsal sensilla distinct only on segments III,IV, absent on V. Hairs 1,3-5-I-VII on a common plate; hair 2-I-VI mesad of 1, on a distinct circular tubercle on segments II-IV; hairs 1,7,11-VII single, spikelike. *Segment VIII*: Hairs 2-5-VIII arising from a large sclerotized plate; hairs 4,5-VIII single, spikelike. *Siphon*: Short, without acus. Integument moderately pigmented, smooth. Hair 1-S single, spikelike and within basal 0.3. Trachea well developed. *Anal Segment*: Saddle complete, broader than long. Acus absent. Caudal margin with short to moderately long spicules. Hair 1-X on saddle margin, single and spikelike; hairs of dorsal brush (2,3-X) branched; ventral brush with 7 pairs of single, strongly fringed hairs on a boss. Gills short, globose.

SYSTEMATICS. *T. gigantulus* is distinguished from other known Philippine *Toxorhynchites* by the following features: (1) in the adults, by the tawny lateral tufts on abdominal segments VI and VII, (2) in the pupa, by the presence of an accessory hair on the metanotum caudad of 12-C; hair 3-I long and single; hair 6-VII short and double and not reaching the apex of its tergite, (3) in the larva, by the single, spike-like siphonal hair 1-S. As pointed out by Barraud (1934:22), the closest relative of *gigantulus* appears to be *minimus* Theobald, 1905 of Ceylon, India and Sumatra. The latter differs in the adults in the mainly black tuft of abdominal segment VII and in the larva in the double or triple hair 1-S.

BIONOMICS. No data are available as to the source of the collections from which the rearings of this species were made. The breeding sites could have been treeholes, bamboo or leaf axils.

DISTRIBUTION. Apparently endemic to the Philippines, where it has been collected only in Central Luzon. Material examined: 15 specimens; 4 ♂, 2 ♀, 6 pupae, 3 larvae; 6 individual rearings (3 larval, 3 pupal).

PHILIPPINES. *Luzon*: Laguna Province, unspecified locality, 12 Aug 1965, F.E. Baisas et al (UCLA 249), 2 lp♂ (249-22,37), 1 lp♀ (249-44), 2 p♂ (249-103,104), 1 p♀ (249-101) [UCLA, USNM]. Limay, Bataan Province, Nov 1924, R.C. McGregor, ♂ holotype (Dyar and Shannon 1925: 67, USNM). San Andales, Rizal Province, Dec 1926, R.C. McGregor, 1 ♂ (Bohart 1945:24, USNM).

REFERENCES CITED

Barraud, P.J.

1934. Family Culicidae. Tribes Megarhinini and Culicini. London, Taylor and Francis. 463 p. (Fauna of British India, Diptera, v.5)

Belkin, J.N.

1962. The mosquitoes of the South Pacific. v.1. Berkeley, Univ. Calif. Press. 608 p.

Bohart, R.M.

1945. A synopsis of the Philippine mosquitoes. U.S. Navy, Navmed 580. 88 p.

Dyar, H.G. and R.C. Shannon

1925. The types of Philippine mosquitoes described by Ludlow and other notes on the fauna. *Insecutor Inscitiae Mens.* 13:66-89.

Edwards, F.W.

1932. Diptera fam. Culicidae. *In* P. Wytsman, *Genera Insectorum*, Brussels, Desmet-Verteneuil, Fasc. 194. 258 p.

Stone, A. and K.L. Knight

1957. Type specimens of mosquitoes in the United States National Museum: VI, Miscellaneous genera, addenda and summary. *Wash. Acad. Sci., J.* 47:196-202.

Stone, A., K.L. Knight and H. Starcke

1959. A synoptic catalog of the mosquitoes of the World (Diptera, Culicidae). *Wash., Entomol. Soc. Amer.* (Thomas Say Found. Publication 6). 358 p.

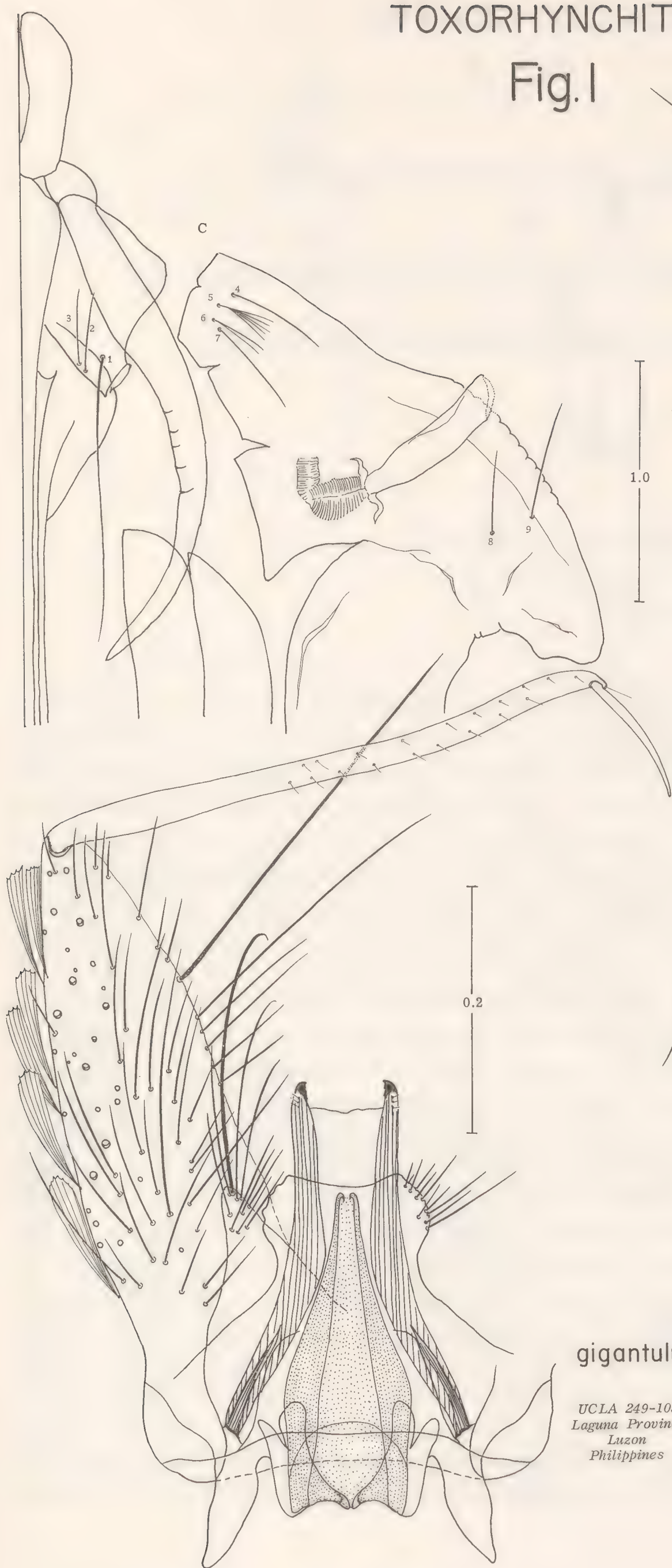
FIGURES

Fig.1. *Toxorhynchites (T.) gigantulus*; male genitalia and pupa.

Fig.2. *Toxorhynchites (T.) gigantulus*; larva.

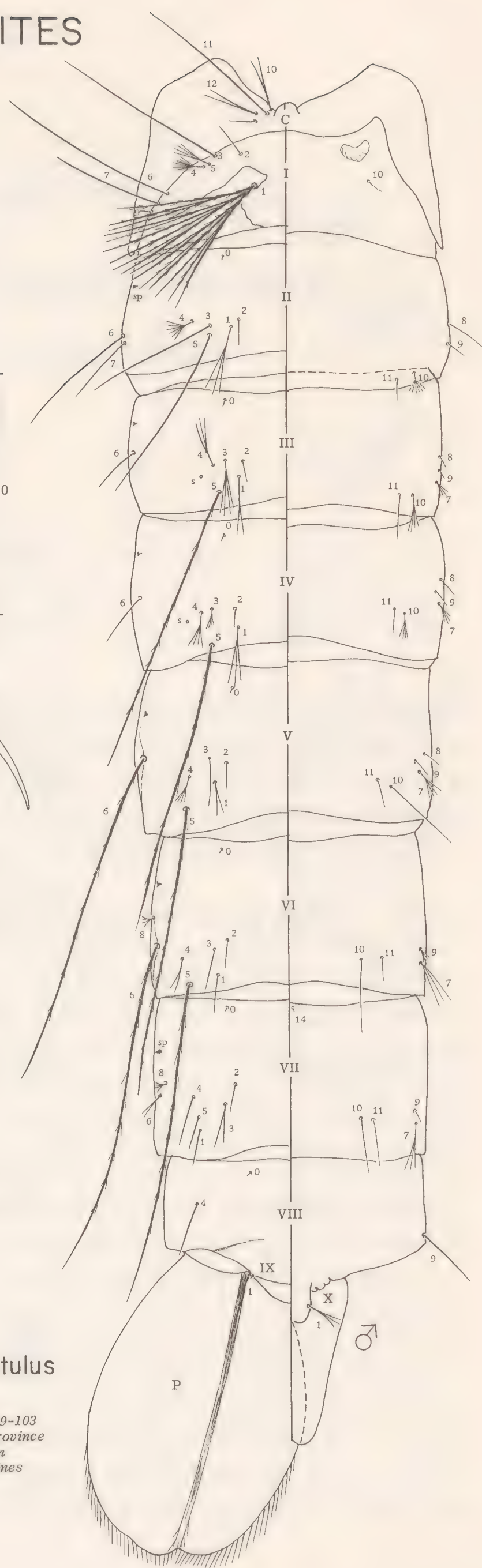
TOXORHYNCHITES

Fig. I



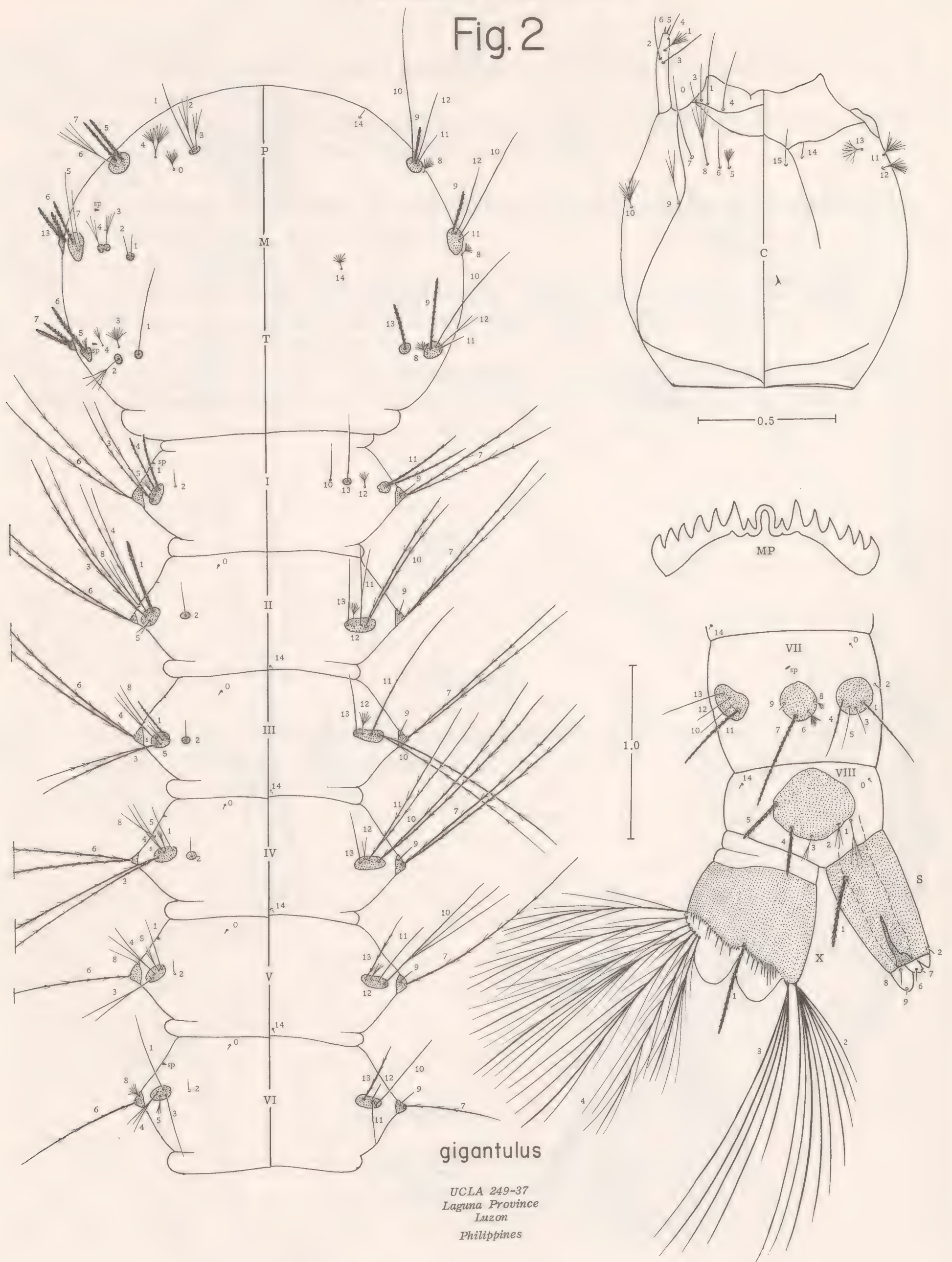
gigantulus

UCLA 249-103
Laguna Province
Luzon
Philippines



TOXORHYNCHITES

Fig. 2



MOSQUITO STUDIES (Diptera, Culicidae)

XV. A NEW SPECIES OF TREEHOLE BREEDING ANOPHELES FROM THE SOUTHWESTERN UNITED STATES¹

By

Thomas J. Zavortink²

During the past 3 years a large number of specimens of the *Anopheles* commonly found breeding in treeholes in southern Arizona has been acquired by the project "Mosquitoes of Middle America." Examination of this material has shown it to be a species near, but distinct in all stages from, *Anopheles barberi*. This species, *judithae*, is described and illustrated in the present paper. To facilitate its separation from *barberi*, that species is redescribed and illustrated.

Terminology and format of the present paper are those of Belkin (1962, 1968). Abbreviations used for the references follow the "American Standard for Periodical Title Abbreviations" (Amer. Stand. Ass., 1964). The descriptions of the male genitalia and immature stages of *barberi* and *judithae* are restricted to features not shown in the drawings, such as color pattern and variations, and to characters which serve to separate the 2 species from each other. Since the adults are not illustrated, descriptions of them are somewhat more extensive and contain characters which should serve to separate the species from each other, from other treehole breeding *Anopheles*, and from the remaining New World *Anopheles*. The drawings of the preimaginal forms of each species show the modal condition for the position, length and branching of the hairs. Since a mature fourth instar larva of *barberi* in condition suitable for drawing was not available during this study, the outline of the larval drawing for that species was copied from *judithae*. The pecten teeth counts for each species include not only the large teeth along the posterior margin of the pecten plate, but also the smaller apical teeth. The spiculation of the larvae is described as it appears at 200 magnifications. The sidepiece indices are the ratio of the length of the sidepiece as measured from base to apex on the ventral surface and the width at the point halfway from the base to the apex. In tabulating the bristles on the anterior surface of the forecoxa, all well-developed setae, including those associated with the

¹Contribution from project "Mosquitoes of Middle America" supported by U.S. Public Health Service Research Grant AI-04379 and U.S. Army Medical Research and Development Command Research Contract DA-49-193-MD-2478.

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coxa-tricchanter joint, have been counted. From the vast literature on *Anopheles barberi*, only a few significant papers dealing with the morphology, ecology and distribution of the species have been cited.

I wish to thank John N. Belkin for reading the manuscript and offering valuable suggestions. I am indebted to Sandra J. Heinemann, Michael J. Nelson and William A. Powder for the rearing and preparation of specimens, Sally Dieckmann for preparing the final plates and Sheila Bernstein for typing the manuscript for offset reproduction. The new species is dedicated to a special friend, Judith A. Bergland.

Anopheles (Anopheles) judithae Zavortink, n.sp.

Figs. 1, 2

TYPES: Holotype ♂ with associated larval and pupal skins (UCLA 302-40), Cochise Stronghold Recreation Area, Dragoon Mountains, Cochise County, Arizona, elevation about 5500 ft, larva from a rot hole in a living evergreen oak tree, 22 Mar 1966, T.J. Zavortink [USNM]. Allotype ♀ with associated larval and pupal skins (UCLA 302-42), same data as holotype. Paratypes: 6 lp♂ (302-25, 41, 43, 45, 46, 48), 5 lp♀ (302-44, 47, 49, 51, 52), 3 p♂ (302-100, 101, 103), 1 p♀ (302-102), 1 ♀, 1 P, 6 L, same data as holotype; 1 lp♀ (306-20), same data as holotype except collected on 23 Mar 1966 (UCLA 306); 1 lp♂ (328-22), same data as holotype except collected on 4 Sept 1966 (UCLA 328); 7 lp♂ (342-13, 15, 30, 33, 38, 43, 44), 11 lp♀ (342-10, 31, 32, 34-37, 39-42), 10 p♂ (342-100-106, 109, 110, 113), 5 p♀ (342-107, 108, 111, 112, 114), 17 ♂, 25 ♀, 48 P, 27 L, same data as holotype except collected on 6 Sept 1966 (UCLA 342).

Anopheles barberi of Vargas (1940:319-322; 1943:64, 65, 66, 67, in part); Jenkins and Carpenter (1946:35-36, in part); Carpenter and LaCasse (1955:32-34, in part); Richards, Nielsen and Rees (1956:14); Vargas and Martinez (1956:111-113, 140, in part); Rigby, Blakeslee and Forehand (1963:50); Burger (1965:396); Nielsen, Arnell and Linam (1967:76); Carpenter (1968:72, in part); Nielsen, Linam, Arnell and Zavortink (1968:363).

FEMALE. Wing: 3.31 mm. Proboscis: 1.92 mm. Forefemur: 2.18 mm. Abdomen: about 2.1 mm. *Head:* Integument light to dark brown; orbital bristles dark brown, interocular bristles amber; dorsum of head with erect scales only, these entirely pale white or a few lateral ones dark; interocular scales numerous, white, usually none appreciably elongate; labium and palpus entirely dark scaled, the proximal scales appressed; torus and first flagellar segment with a few small dark scales. *Thorax:* Mesonotum conspicuously shortened and arched; mesonotum with integument very light to dark brown, largely shining, without a broad hoary median longitudinal stripe; pleural integument lighter or becoming lighter ventrally; mesonotal bristles numerous, strongly developed, long and conspicuous, dark in color except for some amber anterior acrostichals; mesonotal scaling restricted to a small tuft of 5-20 whitish scales in center of anterior promontory and a few erect light or dark scales in prescutellar area; *apn*, *sp*, *pra*, *ppl*, *stp* and upper *mep* bristles or hairs present, those on *ppl* 2-5 in number, those on *stp* in a more or less continuous vertical row; pleuron without scales. *Legs:* Integument of coxae same color as or lighter than adjacent portions of pleuron; anterior portion of forecoxa with 6-18 strongly developed bristles; coxae without scales; femora, tibiae and tarsi entirely dark scaled. *Wing:* Veins and fringe entirely dark scaled, scales on veins uniformly distributed and not grouped into dark spots. *Haltere:* Integument of stem light, knob dark scaled. *Abdomen:* Integument of tergites light to dark brown, usually somewhat dappled, sternites lighter; completely devoid of scales.

MALE. As for female except for usual sexual differences.

MALE GENITALIA (fig.1). *Sidepiece*: More or less cylindrical or short conical, mesal edge nearly straight, length about 1.9-2.6 width; parabasal spines only slightly more strongly developed than internal spine; lateral parabasal spine not flattened preapically, apex gradually attenuate and strongly recurved; internal spine more strongly developed than large setae of sidepiece, apex usually recurved; distance from parabasal spines to internal spine usually 1.5-2.0 distance from latter to apex of sidepiece. *Clasper*: Setae present in basal 0.33. *Proctiger*: Generally extending to about level of internal spine.

PUPA (fig.1). Abdomen: 2.80 mm. Trumpet: 0.37 mm. Paddle: 0.83 mm. *Cephalothorax*: Lightly pigmented with middorsal area, region caudad of trumpet and upper portion of wing case darker. *Trumpet*: Light amber in color. *Abdomen*: Lightly pigmented with anterior and/or lateral portions of segments II-VIII darker; hair 9-II-VIII lightly pigmented, concolorous with integument; 9-III usually about 2.0 diameter and length of 9-II and 0.5 diameter and length of 9-IV; 5-III-VI fine, usually 2,3b; 5-VII usually fine and 2,3b, sometimes thickened and single, but then longer than 9-VII. *Paddle*: Lightly pigmented except for darker midrib.

FOURTH INSTAR LARVA (fig.2). Head: 0.67 mm. Anal Saddle: 0.30 mm. *Head*: Largely tan to brown in color with subantennal area and collar darker and area of imaginal eye lighter; mental plate brown, with 3 or 4 teeth on each side of median tooth; inner clypeals (2-C) closely approximated, separated by a distance less than that between inner and outer clypeals (3-C); outer clypeals usually double (single, double); hair 6-C an elongate seta subequal in length to 4-C, usually located nearly in line with 5,7-C; 14-C multiple, 3-6b (2-8). *Antenna*: Uniformly tan to brown in color or becoming lighter apically; hair 4-A usually 2,3f. *Thorax*: Integument without spicules; plumose hairs strongly developed, with lateral branches long and strongly pigmented; hair 2-P with only a few (2-6) long lateral branches; 9-P,M,T simple; 3,4-T usually single (single, double). *Abdomen*: Integument without spicules; plumose hairs strongly developed, with lateral branches long and strongly pigmented; hair 1-II-VII similarly developed, palmate; 13-II-V,VII usually single (1-3b); 7-VII usually 3b (1-3). *Segment VIII*: Hair 5 usually single (single, double). *Spiracular Lobe*: Pecten plate with 17-19 (15-20) teeth. *Anal Segment*: Spicules on posterior portion of saddle inconspicuous and arranged into short imbricate rows; ventral brush with 15 or 16 (14-17) hairs, the most caudal of which is normally longer than 2.0 length of saddle.

SYSTEMATICS. Vargas (1940:319-322) was the first to note the occurrence of a treehole *Anopheles* in North America west of the continental divide. His record was based on 3 males collected at Imuris, Sonora, Mexico, a site less than 40 air miles south of the Arizona border. This material was identified as *barberi*; although I have not seen the specimens upon which the report was based, I am certain they are conspecific with *judithae*. Richards, Nielsen and Rees (1956:14) first recorded *judithae*, as *barberi*, from Arizona. Their report was based on data supplied by W.A. McDonald, who had studied only 2 young instar larvae which he had collected near Patagonia. Since *judithae* is most conspicuously differentiated from *barberi* in the fourth instar larva, the failure of earlier workers to detect its specific distinctness was probably due in large part to the fact that they did not have this stage available for study.

While *judithae* and *barberi* form a pair of closely related vicarious species, they are easily differentiated in all stages. Adults of *judithae* have numerous white interocular scales, the erect scales of the head largely pale white, the anterior acrostichal bristles amber and accompanied by pale scales, and relatively few bristles on *ppl* and the anterior surface of the forecoxa. Those of *barberi* have the interocular scales reduced

or absent, the pale erect scales of the head largely dingy yellow, the anterior acrostichal bristles dark and usually not accompanied by scales, and relatively numerous bristles on *ppl* and the anterior surface of the forecoxa. The male genitalia of the 2 species differ most conspicuously in development of the parabasal spines. In *judithae* these spines are only slightly stouter than the internal spine and the lateral parabasal spine is not flattened preapically. In *barberi* the parabasal spines are 2-3 times as stout as the internal spine and the lateral one is flattened preapically. The sidepieces also differ in shape; the ramifications of this difference, such as the straightness of the mesal margin, the position of the internal spine relative to the parabasal spines and the apex of the sidepiece, and the level to which the proctiger projects, are indicated in the descriptions. Pupae of the 2 species are most readily separated on the basis of hairs 9-III-VIII and 5-VI,VII. In *judithae* 9-II-VIII is concolorous with the integument and 9-III is more or less intermediate in length and stoutness between 9-II and 9-IV, whereas in *barberi* 9-II alone is concolorous with the integument, 9-III-VIII being darkly pigmented, and 9-III is more similar to 9-IV than 9-II in length and stoutness. Hair 5-VI and usually also 5-VII of *judithae* is fine and divided into branches, while 5-VI,VII of *barberi* is thickened, single and shorter than hair 9 of the corresponding segment. A few specimens from nearly every collection of *judithae* have hair 5-VII thickened and single, but when it is developed in this manner it is longer than 9-VII. The fourth instar larvae of *judithae* and *barberi* differ in a striking number of characters, only the most conspicuous of which are enumerated here. Larvae of *judithae* have the inner clypeals separated by a distance less than that between the inner and outer clypeals, integument of the thorax and abdomen without spicules, strongly developed plumose hairs, hairs 13-II-V,VII and 5-VIII usually single, and spicules of the anal saddle inconspicuous and arranged in imbricate rows. Larvae of *barberi*, on the other hand, have the inner clypeals separated by a distance more than twice that between the inner and outer clypeals, integument of parts of the thorax and abdomen spiculate, weakly developed plumose hairs, hairs 13-II-V,VII and 5-VIII usually triple, and spicules of the anal saddle conspicuous and largely arranged singly.

Anopheles barberi and *judithae* are apparently quite removed from the other tree-hole *Anopheles* placed in the Coelodiaezesis group. Adults of these 2 species differ from *barianensis*, *fausti*, *plumbeus* and *xelajuensis* in the following: (1) interocular scales not forming a conspicuous white elongate tuft, (2) erect scales of head not sharply divided into brilliant white ones mesally and very dark ones laterally, (3) mesonotum conspicuously shortened and arched, giving a *Culex*-like aspect, (4) mesonotum without a conspicuous broad hoary median longitudinal stripe and (5) acrostichal scaling of mesonotum much reduced. They differ from all of the above-mentioned species except *plumbeus* by lacking light scales in the wing fringe and/or at the apices of the hindfemur and hindtibia. It should be pointed out, however, that two species of treehole breeding *Anopheles* from the western coast of India, *culiciformis* and *sintoni*, which are not placed in the Coelodiaezesis group, agree with *barberi* and *judithae* in all of the features mentioned above.

The larvae of the 2 other New World treehole breeding *Anopheles* differ from *barberi* and *judithae* in a number of characters. Both *fausti* and *xelajuensis* have hair 3-C laterad of 4-C; *fausti* has hair 9-III-VI elongate and plumose and hairs 5,7-VII weakly developed; *xelajuensis* has conspicuous stellate body hairs and does not have palmate hairs.

Larval hair 0-P has not been located on *barberi*, *fausti*, *judithae* or *plumbeus* and is apparently absent. The taxonomic significance, if any, of the presence or absence of this hair is unknown at the present time.

BIONOMICS. The bionomics of *judithae* are summarized in Nielsen, Arnell and Linam (1967:76) and Nielsen, Linam, Arnell and Zavortink (1968:363).

Larvae of this species, like *barberi*, are more frequently found in permanent than temporary treeholes. In southern Arizona the species is common in the high elevation xeric evergreen forest (*Arbutus*, *Cupressus*, *Juniperus*, *Pinus* and *Quercus*), the moderate elevation riparian woodland (*Fraxinus*, *Platanus*, *Populus*, *Salix* and *Sambucus*) and the low elevation gallery forest (*Populus* and/or *Salix*).

DISTRIBUTION. *An. judithae* has been found in Arizona, southwestern New Mexico (Nielsen, Linam, Arnell and Zavortink 1968:363) and Sonora (Vargas 1940:319-322). During this study only the Arizonan specimens cited below have been examined. All this material is in the UCLA collection. Material examined: 810 specimens; 154 ♂, 149 ♀, 279 pupae, 228 larvae; 147 individual rearings (92 larval, 47 pupal, 8 incomplete).

UNITED STATES. *Arizona*: Baboquivari Mountains, Kitt Peak National Observatory, 12 Sept 1968, T.J. Zavortink (UCLA 448), 1 lp♂ (448-27), 6 lp♀ (448-20-25), 1 p♀ (448-15), 1 lp (448-28). Dragoon Mountains, Cochise Stronghold Recreation Area, type series, see above. Nogales (13 mi NW), Calabasas Picnic Ground, 21 Mar 1966, T.J. Zavortink (UCLA 297), 2 lp♀ (297-20,21). Nogales (9 mi NE), 21 Mar 1966, T.J. Zavortink (UCLA 298), 3 lp♂ (298-40,42,49), 4 lp♀ (298-43,45,50,51), 3 p♂ (298-101-103), 4 lp (298-41,46-48), 3 ♀, 4 P, 22 L; same data (UCLA 299), 5 lp♂ (299-21,26,28-30), 6 lp♀ (299-20,23-25,27,31), 1 lp (299-22), 2 L. Patagonia (2-4 mi WSW), Sonoita Creek, 24 Aug 1954, W.A. McDonald (UCLA 137), 2 L; 6 Sept 1963, J. Burger (UCLA 413A), 2 L; 18 Aug 1964, J. Burger (UCLA 253), 17 ♂, 11 ♀; 13 Sept 1964, J. Burger (UCLA 270), 3 L; 20 Sept 1964, J. Burger (UCLA 260), 17 ♂, 7 ♀; 25 July 1965, J. Burger (UCLA 281), 4 L; 27 July 1965, J. Burger (UCLA 282), 5 L; 21 Mar 1966, T.J. Zavortink (UCLA 300), 2 lp♂ (300-30,38), 6 lp♀ (300-32-36,39), 2 p♂ (300-100,102), 2 p♀ (300-101,103), 3 ♂, 3 ♀, 6 P, 12 L; 5 Sept 1966, T.J. Zavortink (UCLA 333), 1 ♂, 1 P, 2 L; same data (UCLA 334), 1 lp♂ (334-15), 4 lp♀ (334-12-14,16), 2 p♂ (334-102,103), 3 p♀ (334-100,101,104), 1 ♀, 3 P, 2 L; 14 Sept 1968, T.J. Zavortink (UCLA 458), 1 p♀ (458-100). Portal (15 mi WNW), 6 Sept 1966, T.J. Zavortink (UCLA 343), 9 lp♂ (343-14,15,17,31-34,36,37), 8 lp♀ (343-12,16,19,30,38-41), 10 p♂ (343-100-104,107,109,110,113,114), 4 p♀ (343-105,108,111,112), 2 lp (343-13,35), 30 ♂, 25 ♀, 69 P, 39 L. Prescott (7 mi NE), 1 Sept 1966, T.J. Zavortink (UCLA 315), 2 lp♂ (315-16,18). Santa Rita Mountains, 20 Oct 1940, R.A. Flock, 1 ♂.

Anopheles (Anopheles) barberi Coquillett

Figs.3,4

1903.*Anopheles barberi* Coquillett, 1903:310. TYPE: Holotype ♀, Plummer's Island, Maryland, 17 Aug 1903, H.S. Barber (USNM, 6959).

Anopheles barberi of Dyar (1904:243-244; 1928:454); Vargas (1942:329-331; 1943:64,65,66,67, in part); Matheson (1944:114-115); Jenkins and Carpenter (1946:35-36, in part); Darsie (1949:524-525); Penn (1949:65-66); Carpenter and LaCasse (1955:32-34, in part); Vargas and Martinez (1956:111-113,140, in part); Carpenter (1968:72, in part).

Coelodiaezis barberi of Howard, Dyar and Knab (1917:1036-1038).

FEMALE. Wing: 3.49 mm. Proboscis: 1.73 mm. Forefemur: 2.10 mm. Abdomen: about 2.2 mm. Very similar to *judithae* but differing in the following features. *Head*: Interocular bristles dark or amber; erect scales on dorsum of head dingy yellowish mesally, dark or dingy yellowish laterally; interocular scales absent or very few. *Thorax*: Anterior acrostichal bristles dark in color; center of anterior promontory usually without scales, sometimes with 1-4 narrow dark scales; *ppl* bristles 7-11. *Legs*: Anterior forecoxal bristles 20-28.

MALE. As for female except for usual sexual differences.

MALE GENITALIA (fig.3). *Sidepiece*: More or less elliptical, mesal edge usually distinctly convex, length about 1.7-2.1 width; parabasal spines much more strongly developed than internal spine; lateral parabasal spine flattened preapically, apex sharply attenuate and recurved or sinuous; internal spine not more strongly developed than large setae of sidepiece, apex usually sinuous; distance from parabasal spines to internal spine about 0.8-1.0 distance from latter to apex of sidepiece. *Clasper*: Usually without setae in basal 0.33. *Proctiger*: Usually extending to near level of apex of sidepiece.

PUPA (fig.3). Abdomen: 3.04 mm. Trumpet: 0.37 mm. Paddle: 0.88 mm. *Cephalothorax*: Moderately pigmented, with dark areas a little more extensive than in *judithae*. *Trumpet*: Deep amber in color. *Abdomen*: Moderately pigmented, with dark areas somewhat more extensive than in *judithae*; hair 9-II moderately pigmented, concolorous with integument, 9-III-VIII darkly pigmented, strongly contrasting with integument; 9-III usually approaching 9-IV in both diameter and length; 5-III-V fine, usually single; 5-VI,VII thickened and single, shorter than hair 9 of corresponding segment. *Paddle*: Moderately pigmented except for darker midrib.

FOURTH INSTAR LARVA (fig.4). Head: 0.65 mm. Anal Saddle: 0.27 mm. *Head*: Largely brown in color with pattern of pigmentation as in *judithae*; mental plate dark brown, usually with 5 or 6 (4-6) teeth on each side of median tooth; inner clypeals (2-C) widely spaced, separated by a distance greater than 2.0 that between inner and outer clypeals (3-C); outer clypeals usually single (single, double); hair 6-C a short pointed peg only about 0.1 length of 4-C, located far caudad of 5-C; 14-C single (single, double). *Antenna*: Uniformly brown to dark brown in color or with apex lighter; hair 4-A single. *Thorax*: Integument, especially on underside of prothorax, spiculate; plumose hairs weakly developed, with lateral branches short and often lightly pigmented; hair 2-P with numerous (more than 8) short lateral branches; 9-P,M,T spiculate; 3,4-T usually 2,3b (1-4). *Abdomen*: Integument on underside of segments I-VIII spiculate; plumose hairs weakly developed, with lateral branches short and often lightly pigmented; hair 1-II usually not palmate, 1-4b, conspicuously less well developed than 1-III-VII when palmate; 1-III-VII palmate, similarly developed or 1-VII smaller; 13-II-V,VII normally 3b (3-5); 7-VII usually single (single, double). *Segment VIII*: Hair 5 usually 3b (2,3). *Spiracular Lobe*: Pecten plate with 12-15 (11-17) teeth. *Anal Segment*: Spicules on posterior portion of saddle more conspicuous than in *judithae* and, for the most part, not arranged into rows; ventral brush with 17 or 18 hairs, the most caudal of which is normally only 1.0-1.5 length of saddle.

SYSTEMATICS. The diagnostic features of this species are indicated above in the description and are discussed in the systematics section for *judithae*. The small series of larvae of this species which has been studied is remarkably uniform except for the development of hair 1-II. This hair varies from a weakly developed simple seta to a well-developed palmate hair. Material from Ohio exhibits this entire range of variation within one collection. While hair 1-VII is palmate in all specimens examined during this study, it may not always be developed in that manner (Howard, Dyar and Knab 1917:1036-1038; Dyar 1928:454).

BIONOMICS. The bionomics of this species are summarized in Jenkins and Carpenter (1946:35-36) and Carpenter and LaCasse (1955:32-34).

The immature stages are more frequently found in permanent treeholes in association with species of *Orthopodomyia* and *Toxorhynchites* than in temporary treeholes along with species of *Aedes*. Two collections made in Ohio in December of

1967 suggest that the 2 species of *Orthopodomyia* inhabiting the eastern United States, *alba* and *signifera*, may select different types of permanent treeholes for oviposition and that *barberi* selects the same type as *signifera*. The collections referred to were from horsechestnut trees (*Aesculus hippocastanum*) growing within 40 meters of each other; the relatively shallow, brown-colored water of a hole with a broad opening contained small numbers of *alba*, *barberi* and *signifera* larvae, while the deep, yellow-colored water of a hole with a narrow opening contained several hundred *alba* larvae and a single *signifera* larva.

DISTRIBUTION. *Anopheles barberi* has been found throughout the eastern United States, from South Dakota and New York in the north to Texas and Florida in the south (Carpenter and LaCasse 1955:32-34; Carpenter 1968:72). During this study only the material cited below, all of which is in the UCLA collection, has been seen. Material examined: 75 specimens; 17 ♂, 15 ♀, 23 pupae, 20 larvae; 20 individual rearings (15 larval, 3 pupal, 2 incomplete).

UNITED STATES. *Alabama*: Guntersville Lake, 28 May-27 Aug 1942, 3 ♀. Sheffield, 18 Aug 1942, J.N. Belkin, 1 ♀. Wilson Dam, 10 June-19 July 1942, J.N. Belkin, 1 lp♀ (167), 1 p♂ (171), 1 p♀ (168), 2 ♂. *Arkansas*: Little Rock, Little Fourche Bayou, 28-29 Mar 1943, J.N. Belkin, 2 lp (440,448), 3 P. *Maryland*: Baltimore, Patapsco State Park, 17 Oct 1965, W.A. McDonald (UCLA 286), 1 L. Cabin John, July 1965, W.A. McDonald (UCLA 286A), 1 L. *New York*: Ithaca, 18-26 July 1932, R. Matheson, 2 ♂, 3 ♀. *Ohio*: Canton, 22 Dec 1967, T.J. Zavortink (UCLA 437), 10 lp♂ (437-30-36,39,41,43), 4 lp♀ (437-37,38,40,42), 1 p♂ (437-44), 1 L. *Tennessee*: Kentucky Lake, 26 Aug 1942, 1 ♂. *Texas*: Abilene, 30 Aug 1953, R.X. Schick, 2 ♀.

REFERENCES CITED

Belkin, John N.

1962. The mosquitoes of the South Pacific (Diptera, Culicidae). v.1. Berkeley, Univ. Calif. Press. 608 p.

1968. Mosquito Studies (Diptera, Culicidae). VII. The Culicidae of New Zealand. Amer. Entomol. Inst., Contrib. 3(1). 182 p.

Burger, John F.

1965. *Aedes kompi* Vargas and Downs 1950, new to the United States. Mosquito News 25:396-398.

Carpenter, Stanley J.

1968. Review of recent literature on mosquitoes of North America. Calif. Vector Views 15:71-98.

Carpenter, Stanley J. and W.J. LaCasse

1955. Mosquitoes of North America (North of Mexico). Berkeley, Univ. Calif. Press. 360 p.

Coquillett, Daniel W.

1903. A new *Anopheles* with unspotted wings. Can. Entomol. 35:310.

Darsie, Richard F.

1949. Pupae of the anopheline mosquitoes of the northeastern United States (Diptera, Culicidae). Rev. Entomol. 20:509-530.

Dyar, Harrison G.

1904. Brief notes on mosquito larvae. N.Y. Entomol. Soc., J. 12:243-246.

1928. The mosquitoes of the Americas. Wash., Carnegie Inst. [Publication 387] 616 p.

Howard, Leland O., H.G. Dyar and F. Knab

1917. The mosquitoes of North and Central America and the West Indies. v.4. Wash., Carnegie Inst. [Publication 159] p.525-1064.

Jenkins, Dale W. and S.J. Carpenter

1946. Ecology of the tree hole breeding mosquitoes of Nearctic North America. Ecol. Monogr. 16:31-47.

Matheson, Robert

1944. Handbook of the mosquitoes of North America. ed.2. Ithaca, Comstock Publishing Co. 314 p.

Nielsen, Lewis T., J H. Arnell and J.H. Linam

1967. A report on the distribution and biology of the tree hole mosquitoes in the western United States. Calif. Mosquito Control Ass., Proc. Pap. 35:72-76.

Nielsen, Lewis T., J.H. Linam, J H. Arnell and T.J. Zavortink

1968. Distributional and biological notes on the tree hole mosquitoes of the western United States. Mosquito News 28:361-365.

Penn, George H.

1949. Pupae of the Nearctic anopheline mosquitoes north of Mexico. Nat. Malaria Soc., J. 8:50-69.

Richards, Charles S., L.T. Nielsen and D.M. Rees

1956. Mosquito records from the Great Basin and the drainage of the lower Colorado River. Mosquito News 16:10-17.

Rigby, Paul T., T.E. Blakeslee and C.E. Forehand

1963. The occurrence of *Aedes taeniorhynchus* (Wiedemann), *Anopheles barberi* (Coquillett), and *Culex thriambus* (Dyar) in Arizona. Mosquito News 23:50.

Vargas, Luis

1940. *Anopheles (Anopheles) barberi* en Mexico. Rev. Inst. Salubr. Enferm. Trop. 1:319-322.

1942. El huevo de *Anopheles barberi* Coquillett, 1903. Rev. Inst. Salubr. Enferm. Trop. 3:329-331.

1943. Los subgeneros Americanos de *Anopheles* (Diptera, Culicidae). *Anopheles (Russellia) xelajuensis* de Leon, 1938 n.subgn. y *Anopheles (Coelodiaezis) fausti* n.sp. Rev. Inst. Salubr. Enferm. Trop. 4:57-77.

Vargas, Luis and Amado Martinez Palacios

1956. Anofelinos Mexicanos. Taxonomia y distribucion. Mexico, D.F., Secretar. Salubr. Asistencia. 181 p.

FIGURES

1. *Anopheles (An.) judithae*; male genitalia and pupa
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ANOPHELES

Fig. I

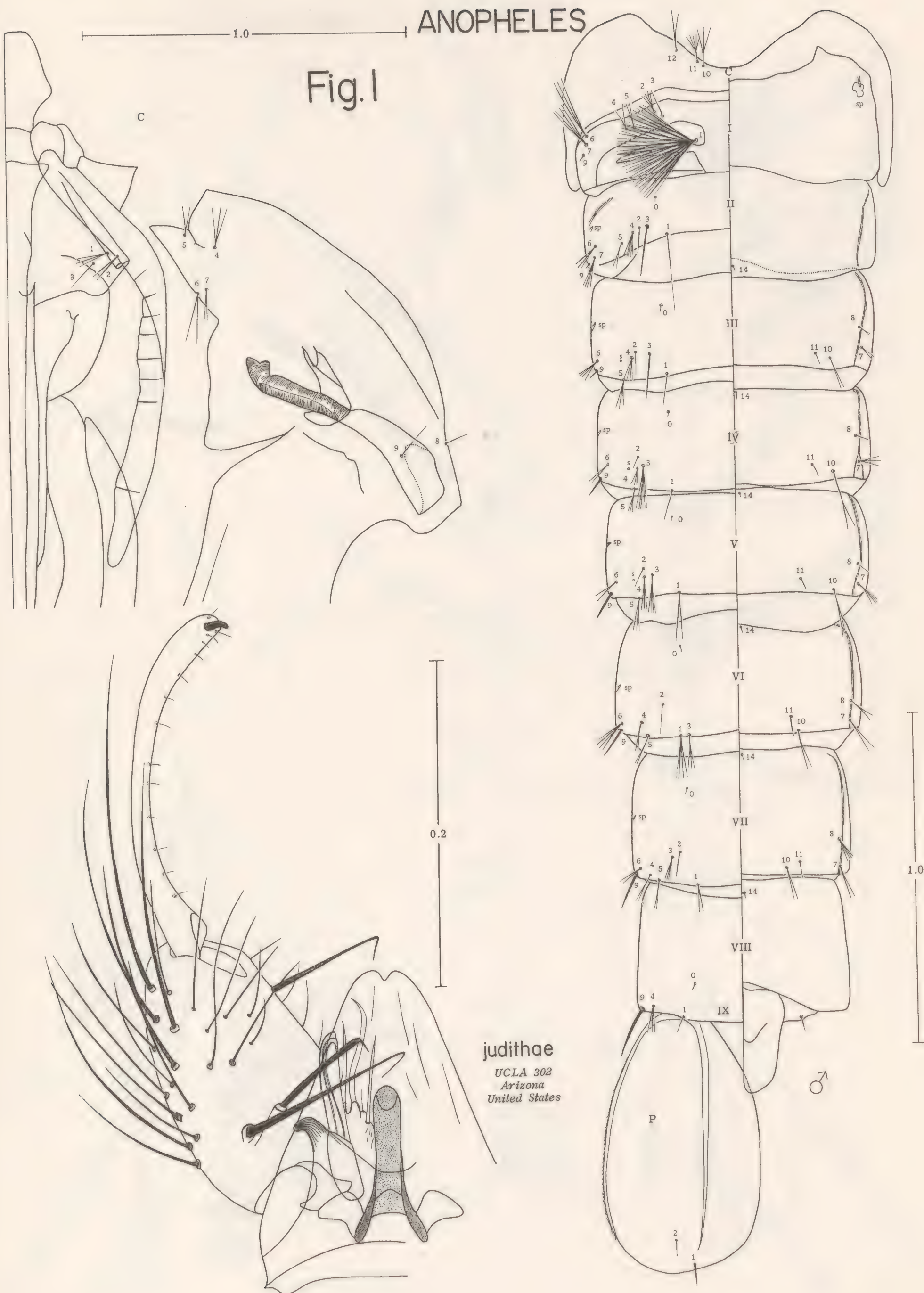
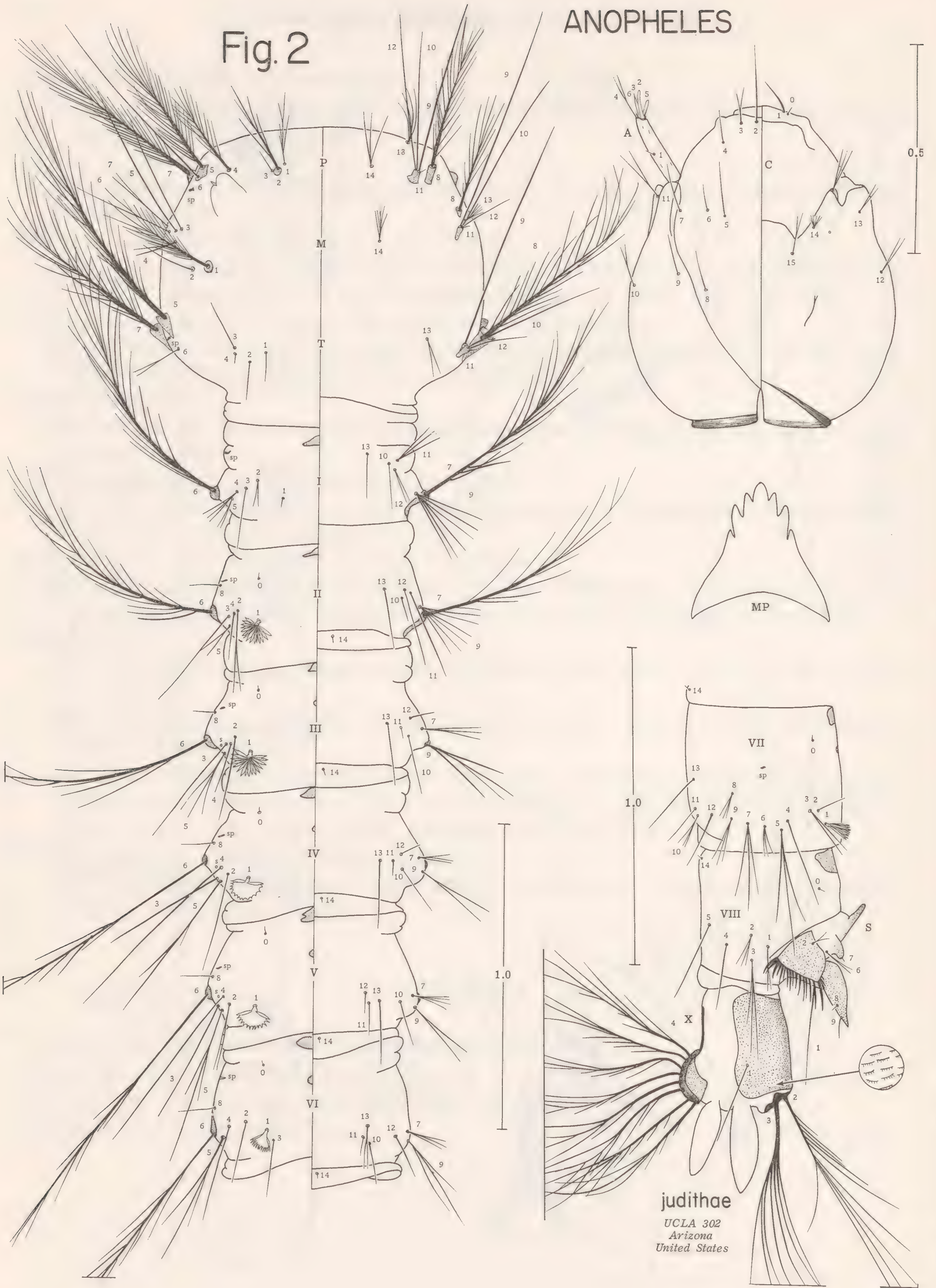


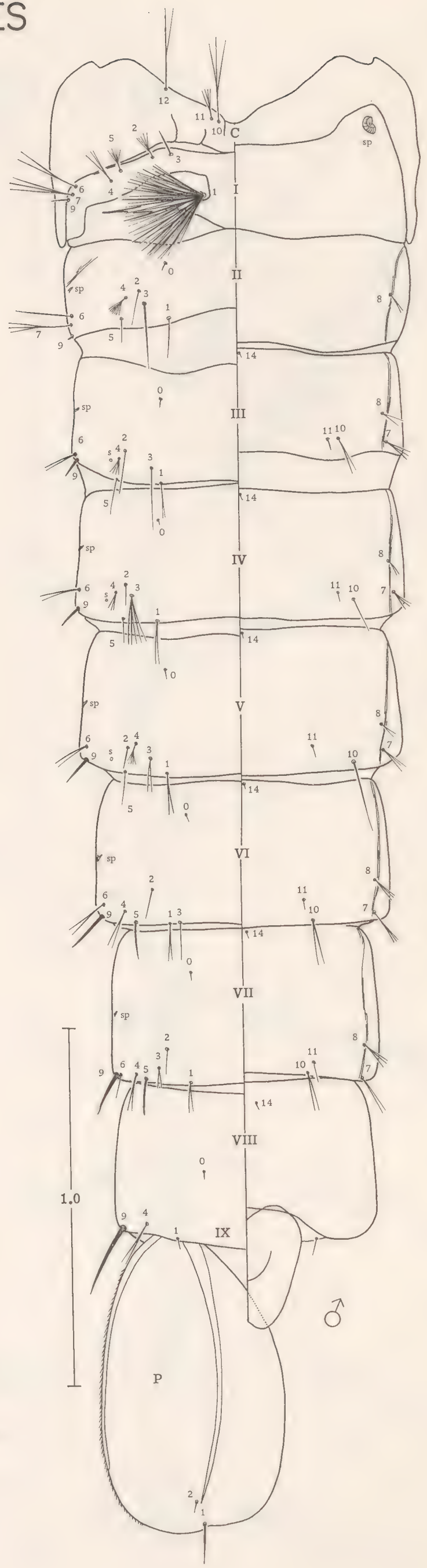
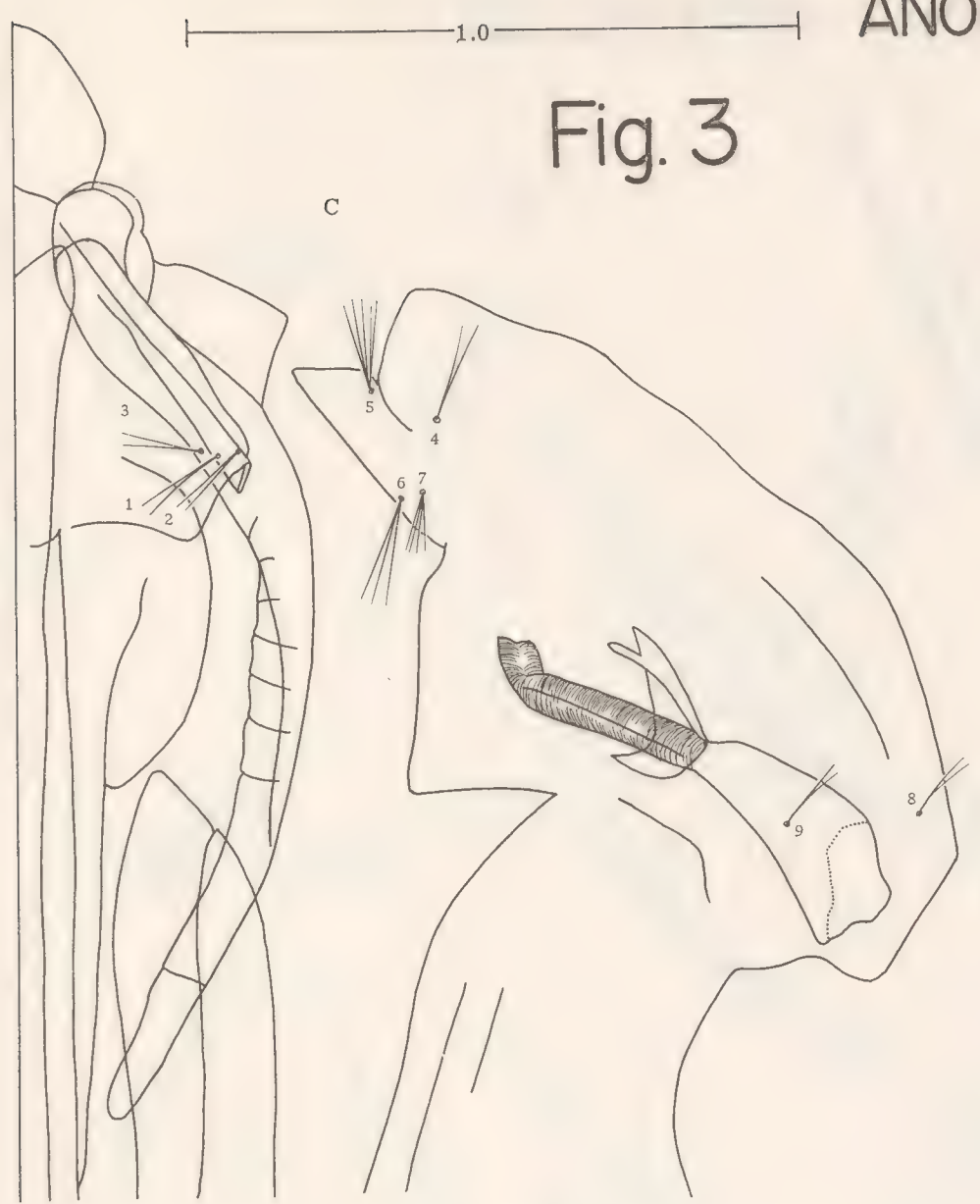
Fig. 2

ANOPHELES



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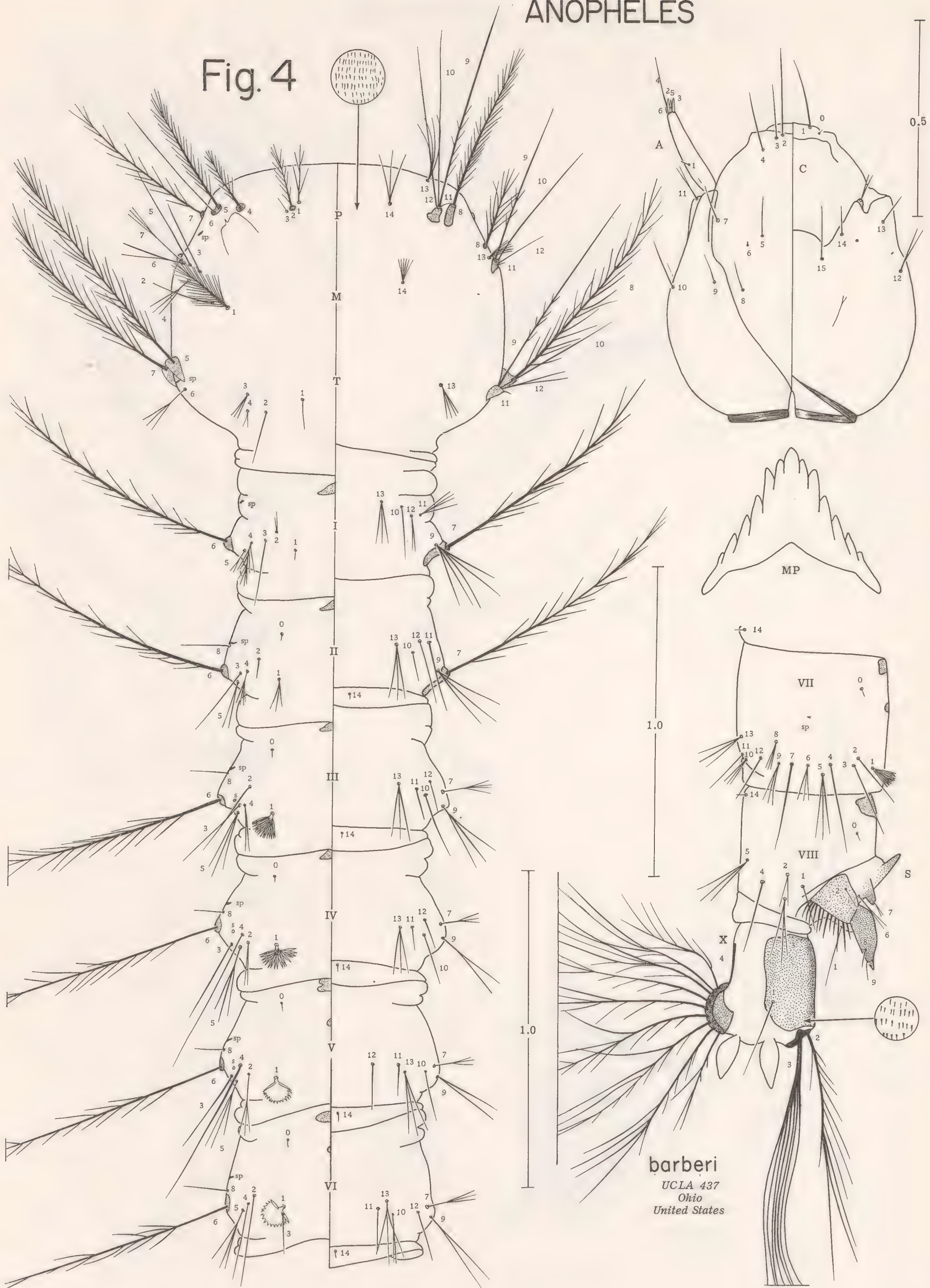
Fig. 3



barberi
UCLA 437
Ohio
United States

ANOPHELES

Fig. 4



(Continued from inside front cover)

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A REVISION OF THE GENUS SPATHIUS IN AMERICA
NORTH OF MEXICO (HYMENOPTERA, BRACONIDAE)

by
Robert W. Matthews



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A REVISION OF THE GENUS SPATHIUS IN AMERICA
NORTH OF MEXICO (HYMENOPTERA, BRACONIDAE)*

By

Robert Wendell Matthews**

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* Submitted to the Department of Biology, Harvard University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

This study is intended as a contribution to the series of systematic studies of the subfamily Doryctinae for the Nearctic Region, initiated by Marsh (1965).

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INTRODUCTION

Spathius is a cosmopolitan genus of Braconidae with over 300 described forms which, with few exceptions, are ectoparasites of wood-boring coleopterous larvae, predominantly Scolytidae. A relatively recent revision of the Old World species exists (Nixon, 1943). For the Nearctic species, the only work to date consists of a few isolated and vague descriptions, and Ashmead's (1893) key to the species (including several newly described ones). This has proved unusable because of several errors and inconsistencies. The 16 described Nearctic species (Muesebeck et al., 1951) have been so poorly understood that identification has been impossible except by comparison with the types.

This revision recognizes 21 species of North American Spathius, of which 11 are described as new. The types of all previously described species have been examined and new descriptions prepared for all valid species. Of the more than 2500 specimens seen, a large proportion represent reared series. In addition to providing host data, these series have permitted positive sex associations and made it possible to more accurately assess intraspecific variation.

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 (CAES)
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U.S. National Museum, Washington, D.C. (USNM)

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Finally, to my wife, Janice, for her patience, aid and understanding throughout my graduate career.

TERMINOLOGY AND SPECIFIC CHARACTERS

The descriptive vocabulary used in the species descriptions is taken largely from Nixon's (1943) revision of the Old World Spathiinae and Marsh's (1965) review of the Nearctic Doryctinae. However, to minimize confusion, diagrams have been prepared illustrating various body parts and showing the points between which measurements have been made.

Measurements were made with the aid of an ocular micrometer, the majority at a magnification of 72x on a Leitz stereoscopic microscope. All quantitative measurements, with the exception of body and wing length, are presented in the form of proportions. Where possible, measurements were taken on at least ten individuals of each sex, selected to represent as wide a geographic range as possible. Care was taken to be as accurate as possible, but it is recognized that differences in viewing angle as well as personal idiosyncrasies of technique will give slightly different results for different workers.

In this regard it is important to adjust the specimen so that the end points of the linear measurement fall in the same focal plane. Drawings of wing venation and male genitalia were prepared from material mounted on slides and projected with a Bio-Scope. All other drawings were made on squared paper with the aid of a squared ocular disc.

HEAD.- In *Spathius*, as in most Doryctinae, the head is slightly broader than long, with the temples broad behind the eyes, giving the head a subcubical shape. The occiput is always completely margined by the occipital carina; in the Nearctic species, this carina is never fused with the hypostomal carina, although such fusion occurs in several species groups of Old World *Spathius*, and is usually correlated with a narrowing of the temples. (One Old World species, *Spathius aristaesus* Nixon, differs from all other *Spathius* in the lack of a completely margined occiput.)

The antennae of *Spathius* are usually slender, filiform, and as long as or longer than the body; the number of segments is highly variable within a species (for example, 25-36 segments in *S. trifasciatus*), and the right and left antennae may differ in number of segments on the same individual. In the descriptions, number of flagellomeres is used and refers to number of flagellar segments only, excluding the scape and pedicel. In the *brachyurus* group, the flagellomeres are characteristically shortened and subcubical, each with a corona of distinctly longer setae at its apex; also the number of flagellar segments in this group is the lowest for any *Spathius*. On close examination under high power, the eyes of most if not all *Spathius* have minute hairs between the facets, these being most obvious in members of the *brachyurus* group.

The maxillary palpus of *Spathius* is six-segmented and typically somewhat elongate, reaching nearly to the mesocoxal cavities. However, the *brachyurus* group exhibits a tendency toward reduction in palpal size, reaching an extreme in *S. brevipalpus*, sp. n. The mandibles are always bidentate, their bases striate ventrally, and are of little taxonomic value.

Head sculpture*, an important species character, is described with reference to four major regions as follows (Figs. 1, 2):

Face: area between clypeus and antennal insertions; it is almost always transversely strigose-granular in Nearctic *Spathius* and of little taxonomic value.

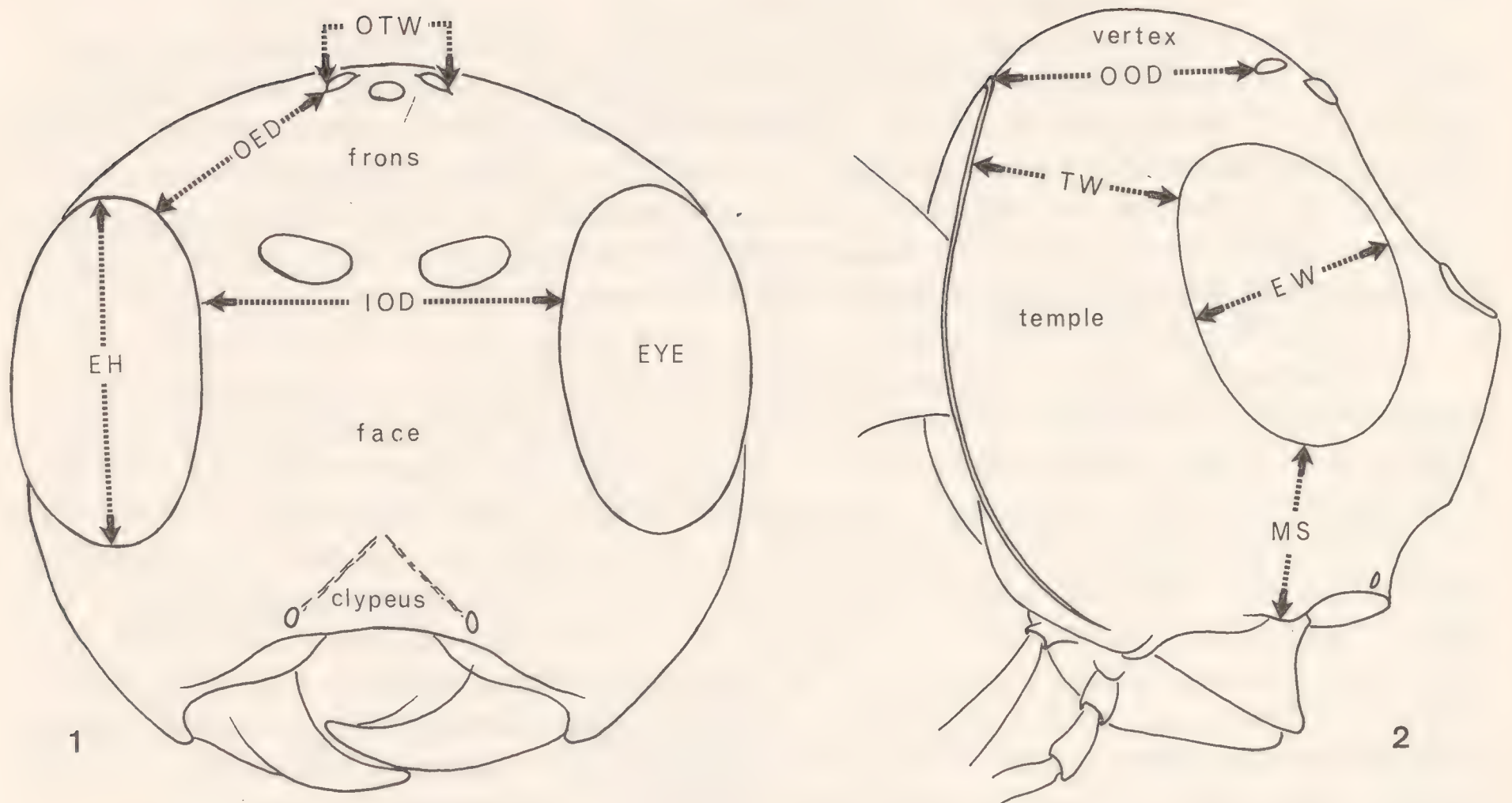
Frons: area between antennal insertions and median ocellus; it has typically transverse striation of varying intensity, but is rugose or smooth in some species.

Vertex: dorsal region of head between lateral ocelli and occipital carina.

Presence or absence of sculpture here is an important species character; when present it usually occurs as transverse striations of varying intensity.

Temples: area between eyes and occipital carina; some Nearctic *Spathius*, in contrast to most doryctines, exhibit fairly prominent sculpturing here.

* Midway in this study Eady (1968) published a paper illustrating types of micro-sculpture in the Hymenoptera and the terminology used to describe them. In general my interpretations are in agreement, and his paper should be consulted for clarification of any descriptive terminology concerning sculpture.



Figures 1 and 2. Head of *Spathius floridanus* Ashmead, frontal and lateral views respectively; explanations of measurements and terminology given in text.

Additional very useful characters are size and position of the eyes and ocelli; following are measurements and abbreviations for expressing these features (Figs. 1, 2):

Eye Height (EH): maximum height (or length) of eye measured in lateral view.

Eye Width (EW): maximum width of eye measured in lateral view.

Malar Space (MS): least distance between lower eye margin and mandible base.

Ocello-eye Distance (OED): least distance between a lateral ocellus and eye margin on same side.

Ocello-occiput Distance (OOD): least distance between occipital carina and a line tangent to posterior margins of lateral ocelli.

Ocellar Triangle Width (OTW): maximum distance between (and including) lateral ocelli.

Temple Width (TW): least distance between occipital carina and posterior dorsal margin of eye.

Interocular Distance (IOD): least width of face along a line just below antennal insertions.

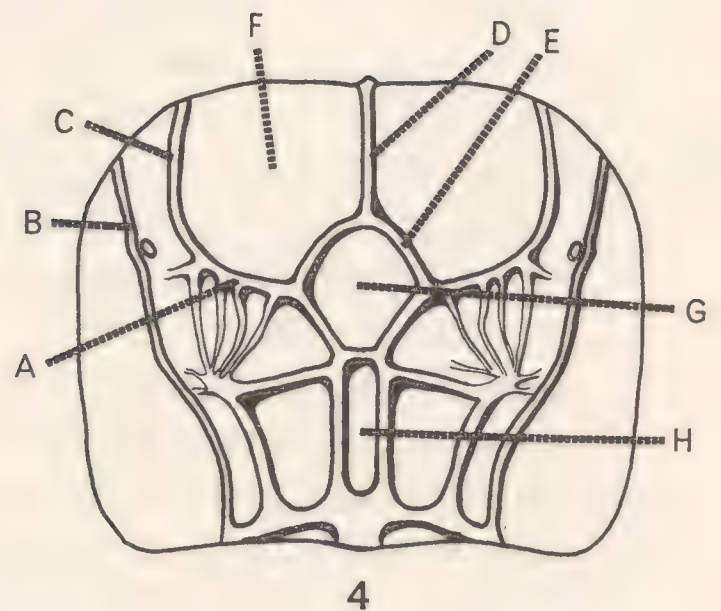
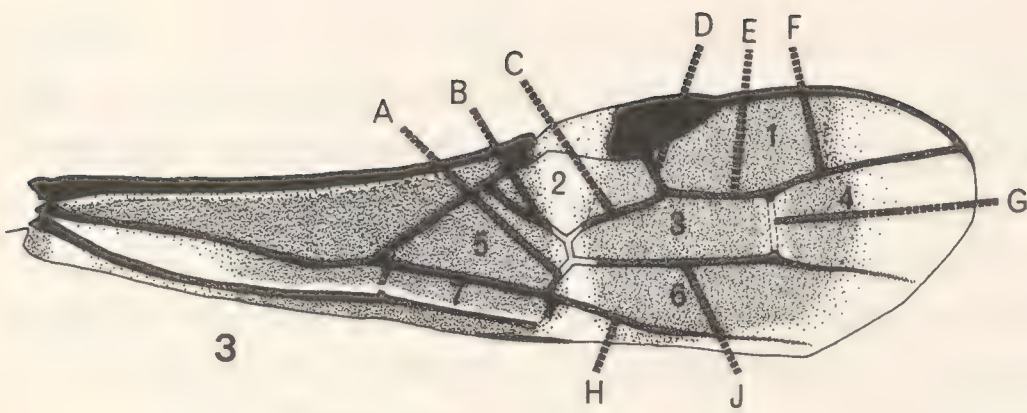


Figure 3. Fore wing of *S. floridanus*, ♀. Veins: A, recurrens; B, first abscissa of cubitus; C, first intercubitus; D, E and F, first, second and third abscissae of radius; G, second intercubitus; H, subdiscoideus; J, second abscissa of cubitus. Cells: 1, radial; 2, 3 and 4, cubital; 5 and 6, discoidal; 7, first brachial cell.

Figure 4. Propodeum of *Spathius marshi*, sp. n. A, costula; B, lateral carina; C, dorsal carina; D, basal carina; E, fork of basal carina; F, dorsal area; G, areola; H, area petiolaris.

THORAX. - The term thorax here means the morphological thorax plus propodeum. Thoracic shape is of some value in species diagnoses. Occasionally a specimen is found which at first appears to be radically different because the thorax is strongly dorsoventrally compressed. These are presumably due to unusually shallow pupation spaces and one must take care not to be misled by them. However, *S. calligaster*, sp. n. is normally strongly flattened (Fig. 17). I have found greatly flattened individuals of three additional species; these are difficult to key because they are so distorted, but otherwise possess the typical species characters. Occasionally, the form and development of the prothoracic "lateral area" (see Nixon, p. 179) is of specific value. However, the position of the "pronotal keel," which Nixon found useful in the Old World *Spathius*, is of little value in the Nearctic forms, being always at least partially fused medially with the posterior margin of the pronotum.

Taxonomically important characters of the thorax include:

1. Mesonotal declivity as viewed from the side.
2. The degree to which the notauli are depressed in a furrow posteriorly.
3. Sternaulus* sculpture and form (for example, compare Figs. 5, 14 and 22).

The mesopleural disc immediately above shows considerable sculptural variation in the Nearctic species, from smooth to strigose to granular to rugose.

4. The prepectal carina crosses the mesosternum anteriorly behind the fore coxae and continues dorsad onto the mesopleuron, forming the posterior border of a roughly pentagonal prepectal area above the fore coxae at the anterior end of the sternaulus (Figs. 5, 14, 17 and 22). The prepectal carina is "incomplete" (Fig. 17) if its expression is obscured at any point along the border of the prepectal area. Sculpture of the prepectal area is also of some specific importance.

* Equals mesopleural furrow in Nixon's and Marsh's terminology.

5. The number and form of the transverse carinae of the scutellar furrow is of specific value in some cases. The scutellar disc is usually granular, but may be rugose or smooth in certain species; the degree to which it is flattened or conically raised (see Fig. 14) is also important.
6. Major carinae of the propodeum, and areas enclosed by them, are indicated in Figure 4. In the European Spathius exarator, relative lengths and degree of development of propodeal carinae have been shown to be highly variable (Beyr, 1961); the same appears true for Nearctic species. However, the shape and sculpture of the enclosed areas, and within broad limits the angle of carinae intersection, appear somewhat more reliable. Also, the posteriolateral angles are occasionally produced to form distinct tubercles or projections which are very useful taxonomically.

LEGS. - The fore tibia bears a row of 10 to 50 stout spines on its anterior edge. Their number and arrangement, while often difficult to see, is of specific value within a broad range, as is a row of as many as 9 spines at the apex of the fore tibia. The outer apical lobe of the hind tibia (see Figs. 18 and 23) usually also bears a row of spines whose number is of specific importance. Frequently, relative lengths of the hind tarsal segments are also useful; however, leg shape is rarely of value except in the males of the trifasciatus group which have the femora considerably swollen (Fig. 15). Presence or absence of a dentiform projection ventrally at the base of the hind coxae may also be of some specific value, although it is variously developed in nearly all the Nearctic forms. The tibiae are banded in the majority of Nearctic Spathius; in some species, however, the bands may be poorly demarcated, the tibiae appearing unicolorous.

WINGS. - Terminology used in reference to Spathius fore wing venation is shown in Figure 3. Presence or absence of infumated wing bands is important, as are relative lengths of first intercubitus and second abscissa of the radius. In addition, the subdiscoideal position, interstitial or not, and differences in cell shapes and proportions, while subtle, are often useful. Males of one Nearctic species, S. stigmatus, sp. n., have a well developed stigma present in the hind wing (Fig. 13); it is of interest that such stigmal development also occurs in several Old World species. Otherwise, hind wings of Nearctic species are quite uniform, but variation occurs in the position of the postnervellus, which if displaced basally divides the mediella into three abscissae; however, this character is highly intraspecifically variable and not reliable.

ABDOMEN. - Numbering of the abdominal segments begins with the first apparent segment (petiole) rather than with the first true morphological segment (propodeum) which for descriptive purposes is here included with the thorax. As used here, the abdomen consists of two main parts, petiole and gaster (segments 2-7). In lateral view, the petiole may be arched (Fig. 5) or nearly straight (Fig. 22); length, while often showing considerable variation, is sometimes of specific importance. Measurement of the petiole is made in dorsal view and expressed as a proportion of the maximum dorsal length of the following segment [tergite (2-3)]. Also, length of the petiolar sternite in relation to total petiole length is of specific value in certain instances.

The first two gastral tergites are not separated dorsally, and I follow Nixon and Marsh in referring to this segment as tergite (2-3). Presence or absence of a thickened lateral margin just below the spiracles on tergite (2-3) is a useful specific character for females; males uniformly possess this thickened lateral margin, which may often be present on subsequent tergites.

Although petiolar sculpture is of little value (see Beyr, 1961), consisting mostly of irregular longitudinal striation, sculpture of the gaster is an impor-

tant character. Its form and expression may, however, vary somewhat both within and between the sexes of a given species. Usually sculpture, when present, is confined to the basal portion of tergite (2-3) but in *S. calligaster*, sp. n. much of the gaster is coarsely granular. If sculpture occurs on tergites 4 to 7, it is usually in the form of fine punctulation. The epipleura of the tergites, defined as that part of the tergites ventral to the spiracles and covering the lateral face of the abdomen, may also show fine punctate or shagreened sculpture in some species.

Male genitalia of all known species were examined in the course of this study, but on the whole are rather uniform and few useful characters were noted. Differences in number, arrangement and relative lengths of the paramere setae, size and shape of basal ring, and relative length of aedeagal apodemes may prove to be of use in distinguishing males of some species.

SIZE, COLOR AND VESTITURE. - Because it is not influenced by head position and abdominal distension, fore wing length (FWL), measured from the free edge of the tegula to the apex of the wing, is given in the descriptions as a more reliable indication of size than body length (BL); for the same reason, ovipositor sheath length (OSL)* is expressed as a proportion of wing rather than of body or abdomen length.

For the most part, the chief diagnostic value of color lies in the arrangements and patterns produced, such as the banded hind tibiae, so that attempts to use exact color terminology would only make the descriptions more cumbersome while adding little to their usefulness. Considerable intraspecific variation in body color may occur in many species and is specifically noted in those cases.

Although Nixon made extensive use of vestiture characters, especially relative length of dorsal hairs of the hind tibia, little variation of this nature was found to occur in the Nearctic forms.

GENERAL REMARKS. - Many species of *Spathius* described by Ashmead (1893) were based on specimens reared by A. D. Hopkins. The previous year Hopkins (1892) had published a list of his bred parasites in *Insect Life*, using Ashmead's manuscript names. Hopkins' original manuscript for this paper is on file in the U. S. National Museum; it is identical to the published version except that Hopkins' specimen label numbers are listed next to the species names. Association of specimens and numbers has been of crucial importance in this revision since most of Hopkins' specimens (and consequently Ashmead's types) have no labels other than this number, and in some cases several specimens have the same number. Hopkins' manuscript has thus often been the sole means for determining which specimens Ashmead had before him and for associating specimens with host and rearing data. Associated insects, host trees and other data (locality, date of emergence, etc.) are recorded on cards filed by number in the U. S. National Museum. I have made extensive use of this Hopkins card file as well, and have listed the Hopkins numbers in the species discussions where they were sources of host or other information.

Much of the confusion so long surrounding the identity of the described Nearctic *Spathius* species can be traced to Ashmead's (1893) descriptions and key. The major characters he used were body color, wing infumation pattern and ovipositor length, the first two of which have proved totally inadequate. Furthermore, his often hurried work resulted in considerable carelessness and inconsistency. For example, his key couplet to *S. unifasciatus*

* Ovipositor sheath length was measured rather than ovipositor length per se because the apparent ovipositor length depends greatly upon angle of extrusion.

(= trifasciatus Riley) states "ovipositor twice the length of abdomen", a fact contradicted by both his own formal description of the species and by examination of the type. At another point he states that S. laflammei Provancher has an ovipositor twice its body length; even if Ashmead had not seen the type, Provancher's description clearly states "Tarriere presque aussi longue que le corps" (Provancher, 1880, p. 164).

Genus SPATHIUS Nees

Spathius Nees, 1818, Nova Acta Acad. Caesar. Leop. Carol. 9: 301.

Type: Ichneumon exarator Linnaeus. Monobasic.

Stenophasmus Smith, 1859, J. Linn. Soc. Lond. 3: 169.

Type: Stenophasmus ruficeps Smith. Monobasic.

Euspathius Foerster, 1862, Verh. naturh. Ver. preuss. Rheinl. 19: 236.

Emendation of Spathius.

Rhacospathius Cameron, 1905, Spolia zeylan. 3: 86. Type: Rhacospathius striolatus Cameron. Monobasic.

Head subcubical, variously sculptured; occiput margined; ocellar triangle with base usually longer than sides, rarely equilateral; first flagellar segment at least as long as second, usually slightly longer; flagellum with 16 or more segments; fore and mid tibiae with 10-55 spines along anterior edge and a row of 4-11 at apex; outer apical lobe of hind tibia with a row of 0-9 spines; fore wing with 3 cubital cells, the recurrent vein entering the second cubital cell; subdiscoideus leaving first brachial cell above middle, occasionally interstitial with discoideus; submediellan cell present in hind wing but short, second abscissa of mediella always longer than first; hind wing of males occasionally with stigma-like thickening at junction of costella, basella and radiella veins; first abdominal tergite lengthened, petiolate, usually abruptly dilated at apex; gaster smooth or variously sculptured, sculpture when present often confined to tergite (2-3); tergite 7 with area of close longitudinal striation on basal half, this area often hidden by overlapping margin of previous tergite; epipleura of tergite (2-3) always fused in females, but separated in males*; ovipositor variable in length but always at least half as long as gaster; male genitalia as in Figure 20.

Discussion. - The essential characters by which Spathius may be distinguished from all other Doryctinae are: (1) abdomen petiolate, the first abdominal tergite lengthened and usually abruptly dilated at apex; (2) fore wing with three cubital cells, the recurrent vein always received into the second cubital cell; and (3) the subdiscoideus always originating above middle of first brachial cell.

The condition of the epipleura of tergite (2-3) - fused in females and divided in males - is somewhat unique to Spathius. Separation of the epipleura of tergite (2-3) in both sexes is characteristic of most other doryctine genera (about 90%, Marsh, in litt.). The adaptive significance of fusion versus division is not understood.

Additionally, the position and form of the stigma in the male hind wing of some species is unusual, being a thickening at the junction of the costella, radiella and basella veins (Fig. 13; see also S. erigone Nixon, 1943, p. 290).

* Nixon (1943) apparently overlooked the separated epipleura of the males, stating in his generic description that the epipleura are always fused.

In most doryctines having stigmal development in the male hind wing (e.g. *Acrophasmus*, *Heterospilus*) the stigma is a large thickening along the costal margin and the other veins are greatly reduced or absent (see figures in Marsh, 1965).

Until quite recently, *Spathius* and its relatives were recognized as a separate subfamily, the Spathiinae. Both Nixon (1943) and Marsh (1965) have adequately reviewed the history of the classification of *Spathius* and related genera, particularly those of the stephaniscine complex. (For a review of the classification and phylogeny of the entire Braconidae see Tobias, 1967.) In his comprehensive review of the Nearctic Doryctinae, Marsh (1965) has included *Spathius* and all of the stephaniscine complex in his redefined Doryctinae, based upon "similarities among these groups in wing venation, fore tibial spines, male genitalia and general morphology". Tobias (1967) concurs, but regards the group as a supertribe, Doryctina, in his subfamily Braconinae.

As the situation now stands, I am in general agreement with Marsh and Tobias. However, having seen a considerable sample of unnamed Neotropical doryctines, a large proportion having the typical "*Spathius*" facies, I am convinced that the present system still leaves much to be desired. It is apparent that the spathiines have radiated extensively in the Neotropics, the diversity being perhaps greater than that found by Nixon in the Old World Malayan Archipelago, which he regarded as the center of distribution for the genus. At present, there are some 7 species of *Spathius* described from the Neotropics (not including several from the West Indies which are discussed by Matthews and Marsh, 1969). While much like typical *Spathius*, all differ in having the recurrent vein received by the first cubital cell and the subdiscoideus arising below the middle of the brachial cell; this venation is widespread among Neotropical "*Spathius*". In addition, I have found at least three other distinct venational types, including the typical form. These anomalies can be dealt with only after further study. For these reasons, conclusions on generic, tribal and subfamily limits in this complex must await redefinition of the Doryctinae based on more thorough knowledge of the world fauna, as classifications based primarily upon north temperate faunas are proving increasingly inadequate. For the same reasons, I prefer to defer the question of the generic affinities of *Spathius*. Both Nixon and Marsh regard *Rhaconotus* Ruthe as the closest relative of *Spathius*. However, as Nixon pointed out, the blister-like swelling on the front and middle femora and the unfused epipleurites of tergite (2-3) characteristic of the *Rhaconotus*-*Platyspathius* complex are not at all typical of *Spathius*.

Paleontology. - Four spathiine fossil species from the Tertiary have been described - three from Rott by Statz (1936, 1938) and a fourth, Scudder's *Ichneumon petrinus*, noted by Brues (1910). Through the courtesy of Dr. Charles L. Hogue, Senior Curator of Entomology at the Los Angeles County Museum, I have been able to study Statz's *Spathius* types. The wings of *S. pedicularis* are hyaline and the specimen is beautifully preserved. The fossils of *S. macroradialis* and *S. longicornis* are less well preserved.

Of these three, only *S. pedicularis* is a true spathiine, its venation agreeing with that noted earlier for the majority of Neotropical species, viz., the recurrent vein entering the first cubital cell and the subdiscoideus arising below the middle of the brachial cell. *S. longicornis*, although probably a doryctine, exhibits the wrong petiole shape and venation for *Spathius*. *S. macroradialis* appears to belong to the Opiinae, having the typical venation and petiole shape of that group.

Scudder's (1890, pl. 5, fig. 14) figure lacks sufficient detail for precise placement, and I have not seen his specimen. Judging from his figure, the petiole of *Ichneumon petrinus* does not appear to have the typical spathiine shape. Brues is probably correct, however, in assigning it to the Braconidae.

In over 1,000 blocks of Tertiary and Cretaceous amber currently under study, no spathiines have been found (L. Masner, *in litt.*).

Distribution. - Representatives of *Spathius* are described from every zoogeographic region. According to Nixon (1943) the greatest concentration of species occurs in the Malay Archipelago, the group apparently originating in that region. However, as noted above, there also appears to have been an extensive spathiine radiation in the Neotropical Region. Nixon recognized only 6 species from the Palearctic Region, but was handicapped by not having access to many of the types; more recently, Fischer (1966) has given a key to 12 species occurring in Europe (one new) and at least two others have also been described from the Palearctic Region since 1943. For the Nearctic Region I here recognize 21 species. No Holarctic species are currently known. I have examined the scanty Palearctic material available in the U. S. National Museum, and although the possibility of holarctic distributions cannot be totally ruled out at this time, none of the North American species will successfully run through Nixon's or Fischer's keys.

Because of their parasitism of wood-boring beetles, the chance of accidental introductions is ever present. Indeed, at least 4 foreign species (based on specimens in the U. S. National Museum and Canadian National Collection) have been intercepted in infested wood items at American ports of entry. However, none appear to have become established. One of these, *Spathius vulnificus* Wilkinson, a parasite of bostrichid beetles from India, has been intercepted at no fewer than 4 different ports. Another, *Spathius exarator* Linnaeus, a parasite of anobiids from Europe, has been frequently recovered from imported items.

EVOLUTIONARY TRENDS

Although in a few cases the Nearctic species could be construed to fit certain of Nixon's (1943) groups of Old World *Spathius* (particularly the *exarator*, *elaboratus*, *fasciatus* and *labdacus* groups), none possess the exact combination of characteristics of these groups; where individual North American species show resemblance to Old World species, this has usually been mentioned in the species discussions. For purposes of showing relationships, however, I have divided the Nearctic *Spathius* into the following species groups, which I feel represent more or less natural groupings:

1. The *brachyurus* group: *brachyurus* Ashmead, *brevipalpus*, sp. n., *marshi*, sp. n. and *stigmatus*, sp. n.
2. The *calligaster* group: *calligaster*, sp. n.
3. The *longipetiolatus* group: *longipetiolatus* Ashmead, *elegans*, sp. n. and *evansi*, sp. n.
4. The *sequoiae* group: *sequoiae* Ashmead, *canadensis* Ashmead and *aphenges*, sp. n.
5. The *pallidus* group: *pallidus* Ashmead, *parvulus*, sp. n. *impus*, sp. n. and *comes*, sp. n.
6. The *laflammei* group: *laflammei* Provancher and *benefactor*, sp. n.
7. The *trifasciatus* group: *trifasciatus* Ashmead and *brunneus* Ashmead.
8. The *simillimus* group: *simillimus* Ashmead and *floridanus* Ashmead.

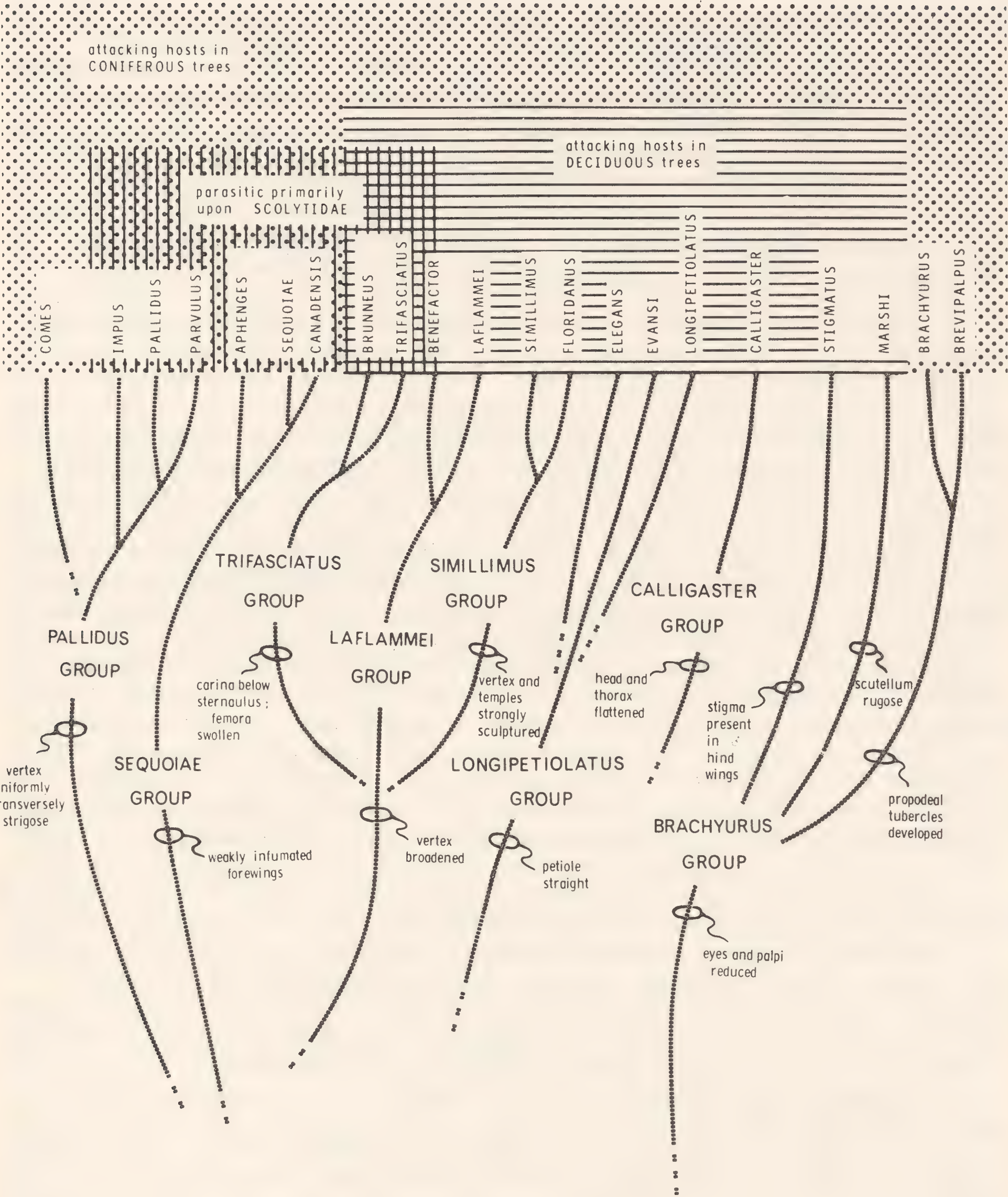


Figure 4A. Possible relationships within the Nearctic *Spathius*. Further explanation in text.

Figure 4A depicts my concept of the relationships among the North American species of Spathius, based upon both morphological and biological characters. Two main lines of descent are apparent, one being that taken by the brachyurus group and the other including the remaining 17 species, within which several distinct evolutionary trends can be recognized.

Members of the brachyurus group are united by the combination of the reduced maxillary palpi, reduced and conspicuously hairy eyes, broad temples, long malar spaces, first intercubitus much shorter than second abscissa of radius, and reduced antennae, the flagellomeres approaching a subcubical shape. The group is clearly specialized, as evidenced by the tendencies toward reduction in maxillary palpi, number of flagellomeres and eye size. The trend toward reduction of the maxillary palpi reaches its extreme in S. brevipalpus, which has apparently completely lost one segment in addition to having the others highly reduced. The brachyurus group does not show clear affinities to any Old World species nor to the remaining Nearctic species. Perhaps it should be given subgeneric or generic rank; however, I prefer to defer such designation until such time as the doryctine fauna is more completely known and generic limits better defined.

Within the brachyurus group, S. brachyurus is apparently the least specialized, having the most nearly normal eyes and the greatest number of flagellomeres; S. brevipalpus seems closely related to brachyurus, both possessing the unique tubercles at the posterior-dorsal-lateral angles of the propodeum and nearly identical body sculpture. Additionally, both are parasites of beetles in pines. The remaining members, S. marshi and S. stigmatus, are both parasites of beetles in deciduous trees, but apparently represent separate evolutionary trends. Of the two, stigmatus is probably the more specialized, having the fewest number of flagellomeres (16-20) of any Nearctic species. Presence of a stigma in the male hind wing, while unique among the Nearctic species, is probably a convergent character, since similar stigma-like thickenings occur sporadically in several Old World species; this character's adaptive significance is not understood. The unique combination of characters possessed by S. marshi, particularly the form of the sternaulus (Fig. 5) and the rugose scutellum, apparently have no parallel in any described Spathius; additionally, the wings are totally hyaline, somewhat atypical for the genus.

The calligaster group is represented only by Spathius calligaster, an isolated species of uncertain affinities; it is characterized by the strongly flattened head and thorax (Fig. 17), coarsely granular sculpture on all but the apical margins of tergites (2-3), 4 and sometimes 5, absence of spines on the outer apical lobes of the hind tibiae, strongly thickened lateral margin of tergite (2-3) and the typically interstitial subdiscoideus vein. The flattened body is convergent with species of Nixon's labdacus group but other characters do not correlate. Biologically it is unique in attacking eucnemid beetles.

The longipetiolatus group includes the largest of the Nearctic species. Except for isolated rearing records from various hardwoods and a single host record (for elegans attacking an anobiid), nothing is known of the biology of this group. The three included species are not closely related, and the group's affinities are uncertain although some characters are shared with the Palearctic exarator group. Available evidence suggests that the longipetiolatus group may be most generalized of the Nearctic groups and probably closest to the ancestral spathiine stock, its members being characterized by relatively large size, long ovipositors (the ♀ longipetiolatus is unknown), and elongate, straight petioles (Fig. 22). The antennae of evansi have the most flagellomeres of any Nearctic species (35-48); it is also one of the most widely distributed of the

of the Nearctic species, occurring from the Rockies eastward.

Members of the laflammei, simillimus and trifasciatus groups appear to be derived from the same basic stock, but have split into three distinct evolutionary lines. All three groups share the relatively wide vertex, a well-developed row of 3-10 spines on the outer apical lobe of the hind tibia, and strongly banded fore wings; additionally, they all attack beetles in deciduous trees. A dominant evolutionary trend in the complex seems to be the acquisition of a relatively wide vertex and broad temples; a general increase in body robustness is also apparent.

The laflammei group seems to represent the basic stock of the complex, with S. benefactor apparently the most generalized member, having the narrowest vertex. It is sometimes hard to distinguish this species from members of the pallidus and sequoiae groups. Both benefactor and laflammei attack weevils and bark beetles in deciduous trees, benefactor being commonly reared from elm.

The trifasciatus group has acquired at least two unique features: the presence of a strong longitudinal carina beneath the sternaulus (Fig. 14) and strongly swollen femora in the males (Fig. 15). The two included species attack closely related species of scolytids, trifasciatus being commonly reared from Scolytus quadrispinosus in hickory and brunneus from S. muticus in hackberry.

As the third group of this complex, the simillimus group is characterized by the very strong uniformly granular-strigose sculpture of the vertex and temples and the usually rugose or wrinkled scutellar furrow carinae. Its two members have become specialized upon a different host assemblage, attacking either cerambycid or buprestid larvae almost exclusively.

All of the members of the sequoiae and pallidus groups have become adapted to beetles attacking conifers, a major ecological shift, and within each group certain secondary trends can also be recognized; the species comprising both groups include some of the smallest and taxonomically most difficult members of the Nearctic fauna. The sequoiae group is characterized by weakly infumated, indistinctly banded fore wings and a nearly smooth to delicately strigose vertex. Of the three included species, S. aphenges is probably the most advanced, with the shortest ovipositor of any Nearctic species (except parvulus), reduced head sculpture, and specialization upon beetles attacking pine cones. S. canadensis and S. sequoiae appear to be quite closely related and possibly subspecies, but more data are needed to resolve that problem; both attack a similar host complex, sequoiae being western in distribution and canadensis being primarily eastern, the ranges overlapping in some parts of western North America.

Members of the pallidus group have the vertex uniformly transversely strigose and have strongly banded fore wings. The three most closely related members - impus, pallidus and parvulus - have relatively narrow vertex and temples, and are parasitic upon scolytids in conifers. S. impus is apparently restricted to Phloeosinus beetles attacking members of the Taxodiaceae and Cupressaceae. S. parvulus and S. pallidus are closely related, parvulus being a smaller species with somewhat reduced mesopleural and vertex sculpture, and a shorter ovipositor; both attack scolytids and curculionids in various species of pine. The remaining species, S. comes, is only tentatively included here; it has broader temples, a longer ovipositor than the others, and has become specialized on buprestids.

The origins and affinities of the Nearctic Spathius fauna are somewhat obscure. The possibility exists that it could have been derived from some as yet unknown Neotropical stock. However, based on material I have seen there appears to be a distinct separation between the faunas of North America

and Mexico, and no species are known from the arid parts of the southwestern United States. This gap may be an artifact of the efforts of collectors, but probably represents a real situation, as the genus is primarily adapted to forested regions. As noted earlier, Neotropical species have certain major differences, especially in wing venation, so that Neotropical origin of the North American species appears unlikely. Instead, the Nearctic Spathius were probably derived from Palearctic elements and the possibility exists that more than one invasion may have occurred.

BIOLOGY

Several isolated studies of the biology of various Spathius species around the world have been made, but the information is too fragmentary for a full-scale comparative consideration of this subject at the present time. For a summary of biological information on Old World species, reference may be made to Nixon (1943). One paper overlooked by Nixon is that of Russo (1938) which includes a discussion of the biology of Spathius rubidus Rossi. Since 1943, two excellent papers by Lyngnes (1955, 1960) on the European Spathius exarator Linnaeus have appeared, which include descriptions of mating and oviposition behavior, larval development, and functional morphology of the female reproductive system; additional more recent papers include a study of the Philippine S. fuscipennis Ashmead (Ishii, 1953) and a brief comparative treatment of internal ovarian morphology of a Japanese species (Iwata, 1959).

For the Nearctic species, published biological information (other than host records) exists only for S. benefactor, sp. n., reported under the name S. canadensis Ashmead; under the description in this paper, work on the life history of this species (Kaston, 1937, 1939; Robert, 1951 a&b, 1960) is summarized briefly. In the following paragraphs, mention will be made of only a few salient general features regarding the biology of Nearctic Spathius.

Host specificity and larval food habits. As ectoparasites upon the larvae of wood-boring beetles, larvae of the genus Spathius are essentially separated in definition from general predators only by consumption of a single host rather than several (Doutt, 1959). In laboratory studies, species have been shown to satisfactorily accept novel hosts, even of a different family than forms their usual diet (Ayyar and Narayananaswami, 1940). Furthermore, the numerous hosts recorded for the more thoroughly studied species cause one to additionally suspect that, in conformity with generally noted evolutionary trends among the ectoparasitic Hymenoptera (see Townes, 1962), the main specializations of Spathius are to the site at which the host feeds rather than to taxon of host.

Broadly, the Nearctic species may be divided into two groups: those which attack beetles in coniferous trees and those which attack beetles in deciduous trees (see Fig. 4A)*. Adaptation to elements within each of these broad ecological zones apparently has been achieved on several independent occasions. For example, species from four different stocks (stigmatus, laflammei, trifasciatus and floridanus) are adapted to attacking beetles in hickory; in pine, three Spathius stocks have converged upon the beetles (2 species each in the brachyurus, pallidus

* Only S. floridanus has been reared from both coniferous and deciduous trees, but it exhibits a decided preference for the latter, attacking several different nut trees (hickory, walnut, chestnut and oaks), and the single record of this species from bald cypress requires further confirmation.

and sequoiae groups). Within the broad division as to tree types, a second grouping may be made, separating those Spathius species which are predominantly parasites of Scolytidae and those attacking non-scolytid borers of several families (see Fig. 4A); however, this division is much less clear-cut. This is not unexpected, since the ovipositing female of each species presumably searches for hosts in a particular ecological niche, there attacking a variety which happen to meet her particular requirements. There are several cases of species attacking both scolytids and curculionids (e.g. brachyurus, sequoiae, benefactor); on the other hand, species attacking the larger borers of the families Cerambycidae and Buprestidae (e.g. simillimus, floridanus) seem somewhat more restricted to these groups. In general, species with shorter ovipositors tend to attack cambial- and bark-inhabiting scolytids and curculionids, while those with longer ovipositors are parasites of beetles which bore deeper in the tree, but there is not necessarily a correlation between ovipositor length and host taxon. (Spathius aphenges is unusual among the Nearctic species in apparently preferentially parasitizing beetles attacking the cones of pine rather than tree trunk and branches.) Another habit which appears to have independently evolved more than once in Spathius is that of multiple oviposition in a given host. I have noted evidence for this situation in at least two North American species (brachyurus, floridanus; see "Biology" for those species), and it is also recorded for S. vulnificus Wilkinson (see Nixon, 1943). It will probably turn up quite commonly as the biologies of more Spathius species become known.

Within the Nearctic Spathius, hosts have been recorded for all but three species (longipetiolatus, evansi and marshi); these are summarized in the accompanying host list. However it must be emphasized that our knowledge of host relations in this genus is still quite incomplete.

Known beetle hosts of Nearctic Spathius species. Sources for the records are given in the species descriptions. Asterisks indicate records of association only; definite parasitization of the named host not established.

Anobiidae

Eucrada humeralis Melsheimer.	laflammei Provancher
Hadrobregmus sp.	elegans, sp. n.

Buprestidae

Agrilus anxius Gory	simillimus Ashmead
A. fallax Say	brunneus Ashmead
A. bilineatus (Weber)	simillimus Ashmead
Chrysobothris femorata (Olivier)	floridanus Ashmead
C. pusilla Castelnau	comes, sp. n.
Chrysobothris sp.	floridanus Ashmead
Melanophila fulvoguttata (Harris)	comes, sp. n.

Cerambycidae

Callidium aereum Newman	simillimus Ashmead
Leptostylus macula Say	*calligaster, sp. n.
Leptura mutabilis Newman	*calligaster, sp. n.
Neichnea laticornis Say	*stigmatus, sp. n.
Xylotrechus colonus (Fabricius)	floridanus Ashmead

Curculionidae

<i>Magdalis armicollis</i> Say	benefactor, sp. n.
<i>M. barbata</i> Say	benefactor, sp. n.
<i>M. inconspicua</i> Horn.	benefactor, sp. n.
<i>M. olyra</i> Herbst	stigmatus, sp. n.
	laflammei Provancher
	floridanus Ashmead
<i>Pachylobius picivorus</i> (Germar)	*brevipalpus, sp. n.
<i>Pissodes approximatus</i> Hopkins	brachyurus Ashmead
	pallidus Ashmead
<i>P. nemorensis</i> Germar	pallidus Ashmead
<i>P. strobi</i> (Peck)	brachyurus Ashmead
	parvulus, sp. n.
<i>Pissodes</i> sp.	sequoiae Ashmead

Eucnemidae

<i>Melasis pectinicornis</i> Melsheimer.	calligaster, sp. n.
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Scolytidae

<i>Carphoborus intermedius</i> Wood	*sequoiae Ashmead
<i>Conophthorus coniperda</i> (Schwarz).	aphenges, sp. n.
<i>Cryphalus</i> sp.	canadensis Ashmead
<i>Crypturgus atomus</i> LeConte	*canadensis Ashmead
<i>Dendroctonus obesus</i> (Mannerheim)	sequoiae Ashmead
<i>D. frontalis</i> Zimmermann	pallidus Ashmead
<i>D. pseudotsugae</i> Hopkins.	sequoiae Ashmead
<i>Dryocoetes affaber</i> (Mannerheim)	*sequoiae Ashmead
<i>D. autographus</i> (Ratzeburg)	brachyurus Ashmead
	canadensis Ashmead
<i>Hylurgopinus rufipes</i> (Eichhoff)	benefactor, sp. n.
<i>Ips avulsus</i> (Eichhoff)	pallidus Ashmead
<i>I. grandicollis</i> (Eichhoff)	pallidus Ashmead
<i>I. latidens</i> LeConte.	aphenges, sp. n.
<i>I. pini</i> (Say)	canadensis Ashmead
<i>Ips</i> sp.	parvulus, sp. n.
<i>Leperisinus aculeatus</i> (Say)	benefactor, sp. n.
<i>Orthotomicus caelatus</i> (Eichhoff)	canadensis Ashmead
<i>Pityophthorus balsameus</i> Blackman	canadensis Ashmead
<i>P. murrayanae</i> Blackman	*sequoiae Ashmead
<i>Pityophthorus</i> sp.	*aphenges, sp. n.
<i>Phloeosinus canadensis</i> Swaine	impus, sp. n.
<i>P. dentatus</i> (Say)	impus, sp. n.
<i>P. punctatus</i> LeConte	sequoiae Ashmead
<i>P. sequoiae</i> Hopkins	sequoiae Ashmead
<i>Phloeosinus</i> sp.	impus, sp. n.
<i>Phloeotribus puberulus</i> LeConte	aphenges, sp. n.
<i>Polygraphus rufipennis</i> (Kirby)	*sequoiae Ashmead
	canadensis Ashmead

<i>Pseudohylesinus nebulosus</i> (LeConte)	<i>sequoiae</i> Ashmead
<i>Scolytus abietis</i> Blackman	<i>aphenges</i> , sp. n.
<i>S. tsugae</i> Swaine	<i>sequoiae</i> Ashmead
<i>S. multistriatus</i> Marsham	<i>benefactor</i> , sp. n.
<i>S. muticus</i> Say	<i>brunneus</i> Ashmead
<i>S. piceae</i> (Swaine)	* <i>sequoiae</i> Ashmead
	<i>canadensis</i> Ashmead
<i>S. quadrispinosus</i> Say	<i>trifasciatus</i> Riley
<i>S. rugulosus</i> Müller	<i>benefactor</i> , sp. n.
<i>S. ventralis</i> LeConte	<i>sequoiae</i> Ashmead
<i>Scolytus</i> sp.	<i>sequoiae</i> Ashmead
<i>Trypodendron lineatum</i> Olivier	* <i>sequoiae</i> Ashmead
<i>Xyloterinus politus</i> (Say)	<i>stigmatus</i> , sp. n.

Diapause. For establishment of a properly functioning host-parasite relationship, the two species obviously must be not only geographically and ecologically, but seasonally coincident as well. Synchronization of development with host is often accomplished in the parasitic Hymenoptera through the mechanism of diapause, but in these groups it is particularly difficult to unravel the causal factors initiating this state (see Doutt, 1959). Those *Spathius* studied appear to attack only the ultimate or penultimate larval instars (Kaston, 1939), but more than one generation per year may commonly be raised upon the same favorable log, and the meagre information available indicates that different species may be either univoltine or multivoltine (see Fiske, 1907; Kaston, 1937, 1939; Robert, 1951a & b, 1960). Overwintering of most Nearctic species probably is in the prepupal stage, as shown for *S. benefactor* in southern Quebec (Robert, 1960) and in Connecticut (Kaston, 1939).

Adult habits and longevity. *Spathius* is a genus of forested habitats, and the free-living adults are practically never found in open or gravelly situations. Adult females apparently spend most of their time crawling over bark in their search for hosts, and probably have a very short preoviposition period following emergence. There is every indication that the genus is normally diurnal, but rarely females of *brachyurus*, *canadensis* and *brevipalpus* have been collected at light.

Adults of both sexes in at least some species feed upon carbohydrates, and while rarely collected from flowers I have often taken them at sources of homopteran honeydew. In the laboratory, adults feed readily upon a sucrose solution or well-soaked raisins. Adults of the Indian species *S. critolaus* Nixon have been kept alive up to 162 days in the laboratory (see review in Nixon, 1943) but probably the adult life is much shorter under natural conditions.

Sexual dimorphism. Among the Nearctic elements of the genus, sexual dimorphism is not particularly pronounced. It is perhaps most evident in males of the *trifasciatus* group, which have strongly swollen femora; although mating has not been observed, this adaptation might be involved in clasping the female. As a general rule, males are smaller and have the sculpture less well developed, except on tergite (2-3) where the sculpture may often be more extensive than in the female. Because extensive courtship displays have never been observed in the parasitic Hymenoptera, it seems more likely that the banded wings of both sexes function primarily in camouflage or mimicry. Held folded over the body, they often give *Spathius* an ant-like appearance from above.

Courtship and mating. As in most other parasites of wood-boring beetles, *Spathius* presumably mate shortly after the female's emergence, probably while still upon the host tree. This is no doubt an important isolating mechanism,

for it would decrease the chance of sympatric allotrophic species encountering one another during this critical time in their life cycle. This feature of its biology, coupled with the apparently rather stereotyped habits of searching for hosts, has important implications for speciation in the genus and may help explain the existence of so many widely sympatric species in eastern North America.

Resource partitioning. Of special evolutionary interest is the occurrence of several *Spathius* species attacking beetles (often of the same species) in the same host tree. For example, at least five species have been reared from beetles infesting hickory, at least three of which have been reported for the same host, *Magdalis olynx* Herbst. Although perhaps not the case in this particular complex, in an analagous situation involving the ichneumonid genus *Megarhyssa*, the three species were found to be almost completely separated by selection of hosts at depths corresponding to the different ovipositor lengths (Heatwole and Davis, 1965). And while recently a number of investigators have doubted the validity of universally applying the competitive exclusion principle, and there is little information on the biology of these sympatric broadly autotrophic *Spathius*, it is possible (but not necessarily probable) that mechanisms exist by which the hosts resources are partitioned spacially and/or temporally. For example, at least one species, *S. stigmatus*, is temporarily isolated, attacking a different beetle assemblage in trees in more advanced conditions of decay (see "Hosts" under *stigmatus*). Other mechanisms - such as different seasons of adult activity, preferences for different stages of the host beetle or different parts of the host tree, or simply different daily activity cycles - probably also exist behind the apparent coexistence of several species.

Key to the North American Species of *Spathius*

FEMALES

- 1. Malar space long, 0.67-1.00x EH; eyes relatively small (Figs. 5, 7 and 8). 2
Malar space 0.33-0.67x EH, usually about half EH; eyes normal (Figs. 2, 17 and 22). 5
- 2. Ovipositor very long, at least twice as long as fore wing; gaster with faint aciculation at base of tergite (2-3). 4. *stigmatus*, new species (p. 32)
Ovipositor not longer than fore wing; gaster smooth and shining, with no trace of sculpture at base of tergite (2-3). 3
- 3. Scutellum rugose; vertex and temples smooth; ovipositor 0.69-0.96x FWL; body in profile as in Figure 5. 3. *marshi*, new species (p. 30)
Scutellum centrally smooth and flat; vertex and temples coarsely granular to rugulose; ovipositor 0.39-0.60x FWL. 4
- 4. Maxillary palpi greatly reduced, at most slightly longer than EH; temples broad, from 1.0-1.3x EH (Fig. 7). 2. *brevipalpus*, new species (p. 29)
Maxillary palpi normal, at least twice as long as EH; temples less broad, from 0.76-1.04x EH (Fig. 8). 1. *brachyurus* Ashmead (p. 26)

5. Sternaulus bounded below by a well developed broadly curved carina extending from prepectal carina to mesocoxal cavity (Fig. 14); scutellum conical in profile. 6
 Sternaulus not as above, typically a simple longitudinal furrow extending from prepectal carina posteriorly for about 2/3 length of mesopleuron and crossed by few to many variously developed ridges (Figs. 17 and 22); scutellum at most slightly conical or projecting apically. 7
6. Ovipositor 0.45-0.68x FWL; head and thorax testaceous; first intercubitus and second abscissa of radius subequal in length; profile of thorax as in Figure 14. 19. brunneus Ashmead (p. 70)
 Ovipositor 0.87-1.20x FWL; head and thorax ferrugineous to piceous; first intercubitus distinctly longer than second abscissa of radius (Fig. 29). 18. trifasciatus Riley (p. 66)
7. Head and thorax strongly dorsoventrally compressed (Fig. 17), the pronotum with a distinct dorsal transverse swelling; tergite (2-3) entirely coarsely granular (except extreme apical margin) and lateral margin thickened over nearly entire length; subdiscoideus vein typically interstitial (Fig. 18). 5. calligaster, new species (p. 35)
 Head and thorax not strongly flattened, or if apparently so then other characters not as above; lateral margin of tergite (2-3) at most thickened on basal half; subdiscoideus arising from upper half of brachial cell. 8
8. Petiole straight, slender and elongate (Fig. 22), usually much greater than 1.5x as long as middle femur; ovipositor long, 1.05-2.1x FWL. . . . 9*
 Petiole usually distinctly arched at base (similar to that shown in Fig. 5) and more stout, always shorter than 1.5x middle femur. 10
9. Ovipositor very long, 1.6-2.1x FWL; hind tarsomere 3 distinctly longer than 5; hind basitarsus not more than 2.1x as long as second tarsomere; antennae with 35-48 flagellomeres. . . 8. evansi, new species (p. 42)
 Ovipositor 1.05-1.55x FWL; hind tarsomere 3 subequal or slightly shorter than 5; hind basitarsus 2.1-2.9x as long as second tarsomere; antennae with 30-38 flagellomeres; propodeum often much lighter than remainder of thorax, distinctly contrasting even to the naked eye. 7. elegans, new species (p. 39)
10. Vertex entirely strongly granular-strigose and very deep (OED/OOD 0.56-0.78, Fig. 24), the sculpture extending undiminished to eyes and over ocellar triangle, frons and entire temples nearly to malar space; scutellar furrow carinae often irregular or rugose. 11
 Vertex not as above, usually narrower (OED/OOD 0.58-1.11) and either entirely or partly smooth (at least adjacent to eyes) or, if apparently completely sculptured, then this in the form of transverse strigosity with little evidence of the granular element; scutellar furrow carinae usually simple and more or less straight. 12

* The unknown female of longipetiolatus Ashmead from Florida will presumably also run out to this point in the key.

11. Gastral tergites 4-6 each with a well developed broad transverse punctulate band anterior to the row of setae; mesopleural disc above and posterior to sternaulus evenly granular to scaly-reticulate; outer apical margin of hind tibia with a row of 4-6 spines, typically 5.
 20. simillimus Ashmead (p. 72)
 Gastral tergites nearly smooth and shining, with at most weak scaly-reticulate sculpture on about basal half of tergite (2-3); mesopleural disc above sternaulus with variously expressed strigosity; outer apical margin of hind tibia with a row of 2-4 spines, typically 3.
 21. floridanus Ashmead (p. 75)
12. Ovipositor very short, 0.32-0.46x FWL; vertex smooth and shining; ratio of petiole length to dorsal length of tergite (2-3) 1.22-1.30; fore wing subhyaline (Fig. 26); western North America.
 11. aphenges, new species (p. 51)
 Ovipositor usually greater than .45x FWL; if shorter, then vertex at least partly sculptured; ratio of petiole length to dorsal length of tergite (2-3) variable, 1.26-2.00; fore wings variously infumated. 13
13. Ovipositor 0.91-1.57x FWL; vertex strongly transversely strigose of uniform intensity from ocellar triangle to occipital carina, becoming granular at eyes; TW/EH 0.63-0.78, and OED/OOD 0.64-0.82.
 15. comes, new species (p. 59)
 Ovipositor shorter, 0.33-1.09x FWL; if ovipositor is greater than 0.91x FWL then either vertex is only faintly strigose, becoming smooth at eyes, or temples and vertex are narrow, TW/EH less than 0.63 and OED/OOD greater than 0.85. 14
14. Outer apical lobe of hind tibia with a row of 6-8 conspicuous spines (Fig. 23); mesopleural disc above sternaulus smooth and shining; body length, exclusive of ovipositor and antennae, 3.5-6.1 mm; antennae with 29-42 flagellomeres. 17. laflammei Provancher (p. 64)
 Outer apical lobe of hind tibia with at most 6 spines, usually 2-5; mesopleural disc variable; smaller species, body length 1.7-4.3 mm; antennae with 20-33 flagellomeres. 15
15. Fore wings weakly infumated to subhyaline (Fig. 28), rarely with complete dark transverse bands; vertex from nearly smooth and shining to delicately transversely strigose; head and thorax usually dark, ferrugineous to piceous; eyes gray, rarely weakly iridescent greenish in white light.
 16
 Fore wings with two dark well defined transverse bands separated by a hyaline band through the basal 1/3 of stigma (Figs. 28-31); vertex variable, sometimes nearly smooth, but often with well developed transverse strigosity; head and thorax testaceous to ferrugineous; eyes typically bright iridescent greenish in white light. 17
16. Ovipositor 0.45-0.65x FWL; tergite (2-3) usually with a distinct area of sculpture on about basal 0.37-0.45, and occasionally with additional sculpture on middle third of tergite and/or weak transverse punctulate bands on some subsequent tergites; body length 2.0-3.8 mm.
 10. canadensis Ashmead (p. 47)

- Ovipositor 0.60-0.80x FWL; tergite (2-3) either nearly smooth or with at most weak mostly obscured sculpture on about basal 0.38 of tergite; body length 2.5-4.1 mm; western North America.
 9. sequoiae Ashmead (p. 44)
17. Vertex very narrow, OED/OOD 0.80-1.11; outer apical margin of hind tibia with at most 4 rather inconspicuous spines, typically 2-3, situated anteriorly (Fig. 18). 18
 Vertex broader, OED/OOD 0.70-0.83; outer apical margin of hind tibia with a row of 3-6 spines. 19
18. Ovipositor 0.35-0.64x FWL; tergite (2-3) with sculpture present on about basal 0.65-0.75; vertex striae delicate, tending to bend medially toward ocellar triangle and blend into its granular sculpture (Fig. 25).
 13. parvulus, new species (p. 55)
 Ovipositor 0.50-1.02x FWL; tergite (2-3) with sculpture on at most about basal 0.40 of tergite, remaining tergites smooth; vertex striae more or less transverse, not notably indented medially.
 14. impus, new species (p. 56)
19. Body color wholly tawny yellow to dirty brown, the gaster beyond basal 2/3 of tergite (2-3) occasionally slightly darker or with darker bands; vertex more or less evenly transversely strigose; mesopleural disc with delicately swirled strigosity above sternaulus.
 12. pallidus Ashmead (p. 53)
 Body color shining ferrugineous, with about apical half of petiole to middle of tergite (2-3) distinctly lighter, suffused with yellow or rufo-testaceous; vertex anteriorly delicately transversely strigose and shining; mesopleural disc above sternaulus smooth and shining or occasionally weakly scaly-reticulate.
 16. benefactor, new species (p. 61)

MALES

1. Scutellum flat, centrally smooth; propodeum with a prominent tubercle projecting from each posterior-dorsal-lateral angle; vertex, temples and mesopleura rugulose. 1. brachyurus Ashmead* (p. 26)
 Scutellum granular or rugose and at least weakly convex; posterior dorsal-lateral angles of propodeum not produced; sculpture of vertex and temples variable. 2
2. Hind wing with a well developed stigma-like thickening at the junction of the costella, basella and radiella veins (Fig. 13); eyes small, the temples broad, TW/EH 0.90-1.04; antennae much shorter than body.
 4. stigmatus, new species (p. 32)
 Hind wing not as above, if apparently with a weak stigma-like thickening then TW/EH less than 0.90 and antennae about as long as body. . . . 3
3. Scutellum rugose; gaster smooth and shining; body in profile as in Figure 5, the propodeum with a distinct tooth-like projection due to the strongly

* The unknown male of brevipalpus, sp. n. will presumably also run to this point.

- protuberant carina separating the areola and area petiolaris.
 3. marshi, new species (p. 30)
 Scutellum evenly scaly-reticulate to granular; gaster variable but often
 with distinct sculpture at least at the base of tergite (2-3); propodeum
 not as above. 4
4. Sternaulus bounded below by a well developed broadly curved carina extend-
 ing from prepectal carina to mesocoxal cavity (Fig. 14); femora strongly
 swollen (Fig. 15); scutellum conical in profile. 5
 Sternaulus not as above, typically a simple longitudinal furrow extending
 from prepectal carina posteriorly for about 2/3 length of mesopleuron
 and crossed by few to many variously developed ridges (see Figs. 17 and
 22); femora not particularly swollen (Fig. 16); scutellum at most slightly
 conical or projecting apically. 6
5. First intercubitus distinctly longer than second abscissa of radius (Fig. 29);
 area where notauli converge rugose and strongly depressed between the
 lateral lobes of mesonotum. 18. trifasciatus Riley (p. 66)
 First intercubitus sub-equal to second abscissa of radius; area of notauli
 convergence shallowly depressed and not strongly rugose.
 19. brunneus Ashmead (p. 70)
6. Head and thorax strongly dorsoventrally compressed (Fig. 17); at least
 tergites (2-3) and 4 uniformly granular (except apical margin).
 5. calligaster, new species (p. 35)
 Head and thorax not strongly dorsoventrally flattened; well-developed
 granular sculpture rarely covering more than basal 3/4 of tergite (2-3).
 7
7. Petiole elongate, slender and nearly straight (Fig. 22), longer than 1.6x
 length of middle femur. 8
 Petiole shorter, usually distinctly arched at base (similar to that shown in
 Fig. 5), always less than 1.55x length of middle femur. 10
8. Antennae with 22-25 flagellomeres; tergite (2-3) with at most weak acicula-
 tion at extreme base; mesopleural disc above sternaulus smooth.
 6. longipetiolatus Ashmead (p. 38)
 Antennae with more than 25 flagellomeres; tergite (2-3) with well-developed
 sculpture on at least basal half; mesopleural disc above sternaulus granu-
 lar to rugose. 9
9. Vertex (and often frons) smooth, shining; sculpture on middle area of
 tergite (2-3) often partially obscured, but when present, always much
 less strongly developed than that of basal half of tergite and separated
 from it by a narrow smooth space; mesopleural disc above sternaulus
 typically scaly-reticulate to irregularly wrinkled.
 7. elegans, new species (p. 39)
 Vertex usually with faint transverse strigosity anteriorly; sculpture of ter-
 gite (2-3) covering about 3/4 of tergite and uninterrupted at middle by a
 smooth space, gradually diminishing in intensity apically; mesopleural
 disc above sternaulus uniformly granular.
 8. evansi, new species (p. 42)

10. Vertex entirely prominently granular-strigose and very wide (OED/OOD 0.56-0.78, Fig. 24), the sculpture extending undiminished to eyes and over ocellar triangle, frons, and entire temples nearly to malar space; scutellar furrow carinae often irregularly wrinkled. 11
 Vertex not as above, usually narrower (OED/OOD 0.60-1.11) and either all or partly smooth (at least adjacent to eyes), or if apparently completely sculptured then this in the form of transverse striation with little evidence of the granular element; scutellar furrow carinae usually simple and more or less straight. 12
11. Gastral tergites 4-6 each with a well developed broad transverse punctulate band anterior to the row of setae. . . 20. simillimus Ashmead (p. 72)
 Gastral tergites nearly smooth and shining, with at most scaly-reticulate sculpture on about basal half of tergite (2-3).
 21. floridanus Ashmead (p. 75)
12. Species occurring west of 100th meridian. 13
 Species occurring east of 100th meridian. 16
13. TW/EH 0.50-0.67; eyes iridescent greenish in white light; fore wings with complete lightly infumated transverse bands (Fig. 30); vertex sculpture, when present, as in Figure 25. . . . 13. parvulus, new species (p. 55)
 TW/EH 0.67-0.85; eyes gray, at most faintly iridescent; fore wings hyaline to weakly infumated in area of radial cell (Figs. 26 and 27). 14
14. Frons nearly smooth, with faint traces of incomplete transverse striation; space posterior to sternaulus smooth to faintly scaly-reticulate.
 11. aphenges, new species (p. 51)
 Frons wholly delicately transversely striate, this sculpture often continuing dorsally onto vertex; space posterior to sternaulus with about 2-6 closely spaced gently curved longitudinal ridges. 15
15. Ratio of lengths of hind tarsus to hind tibia 0.66-0.88; mesopleural disc above sternaulus delicately strigose. . . 9. sequoiae Ashmead (p. 44)
 Ratio of lengths of hind tarsus to hind tibia 0.84-0.96; mesopleural disc above sternaulus scaly-reticulate. . . 10. canadensis Ashmead (p. 47)
16. Vertex distinctly delicately to strongly transversely strigose of more or less uniform intensity from ocellar triangle to occipital carina. . . . 17
 Vertex nearly smooth, or if delicately strigose this only on about anterior half, the part adjacent to occipital carina becoming smooth. 20
17. Sculpture of tergite (2-3) covering no more than basal half of tergite (rarely faint scaly-reticulation beyond middle of tergite); remaining tergites smooth. 18
 Tergite (2-3) with distinct sculpture developed beyond middle, this usually less extensive and of less intensity than sculpture on basal portion; remaining tergites (especially tergite 4) often with distinct punctulation or scaly-reticulation anterior to the setae. 19
18. Temples wide, TW/EH 0.63-0.88; hind tarsomere 2 distinctly longer than tarsomere 5 (not including claw).
 15. comes, new species (p. 59)

- Temples narrow, TW/EH 0.50-0.63; hind tarsomere 2 subequal to tarsomere 5 (not including claw). 14. impus, new species (p. 56)
19. Vertex narrow, OED/OOD 0.80-1.00 (Fig. 25).
 13. parvulus, new species (p. 55)
 Vertex slightly broader, OED/OOD 0.70-0.81.
 12. pallidus Ashmead (p. 53)
20. Outer apical margin of hind tibia with 5-8 strong spines, usually 6 or 7 (Fig. 23); mesopleural disc smooth immediately above sternaulus; vertex wide, OED/OOD 0.58-0.78. . . . 17. laflammei Provancher (p. 64)
 Outer apical margin of hind tibia with 2-5 spines; mesopleural disc sculpture and vertex width variable. 21
21. Eyes usually bright iridescent greenish in white light; mesopleural disc above sternaulus smooth (rarely weakly scaly-reticulate); fore wings distinctly weakly banded, rarely subhyaline. 22
 Eyes dark gray; mesopleural disc above sternaulus scaly-reticulate to delicately strigose; wings typically hyaline, at most weakly infumated in area of radial cell. 10. canadensis Ashmead (p. 47)
22. Vertex narrow, OED/OOD 0.85-1.11; head and thorax predominantly dirty yellow. 14. impus, new species (p. 56)
 Vertex wider, OED/OOD 0.67-0.88; head and thorax predominantly dull ferrugineous. 16. benefactor, new species (p. 61)

1. Spathius brachyurus Ashmead

(Figs. 8, 10)

Rhopalophorus fasciatus Provancher, 1886, Naturaliste can. 16: 129. (nec Spathius fasciatus Walker, 1874, Cist. Ent. 1: 307.) [Type locality: Ontario: Ottawa (lectotype female in Laval Univ., Quebec)].

Eustalocerus fasciatus (Provancher), 1888, Naturaliste can. 18: 378.

Spathius brevicaudus Ashmead, 1892, in Hopkins, Insect Life 4: 258. Nomen nudum.

Spathius brachyurus Ashmead, 1893, Can. Ent. 25: 71, 73. [Type locality: West Virginia: Morgantown (A. D. Hopkins) (lectotype female in USNM, Type No. 2151)].

Spathius dignus Muesebeck and Walkley, 1951, Agriculture Monogr. 2: 169, new name for fasciatus Provancher. New synonymy.

Females: Body length, 3.0-5.3 mm; FWL, 2.3-3.4 mm; ovipositor sheath length, 1.0-1.9 mm. Other measurements and ratios in Table 1.

Head: Antennae short, about as long as FWL; flagellomeres 19-25, those beyond the first subcubical, less than 2x as long as wide, each with a corona of 4 evenly spaced erect setae about 2x as long as all other flagellar setae; eyes sparsely covered with short setae; face coarsely granular to rugose; frons granular to rugose-reticulate, becoming granular in area of ocellar triangle; vertex granular adjacent to ocellar triangle, becoming rugose striate posteriorly; temples rugose striate to coarsely granular; malar space and ocellar triangle finely granular; mandibles striate below at base, the tips dark; maxillary palpi slightly reduced, extending to about posterior border of fore coxae.

Thorax: Lateral areas of prothorax distinct, well developed, delimited by a distinct carina with several cross carinae; remainder of propleura coarsely granular; notauli deeply impressed anteriorly, converging to a slightly depressed rugose-reticulate area; mesonotum abruptly declivous, the lobes evenly granular, the middle lobe often with a weak medial longitudinal furrow; scutellar furrow with 4 to 7 cross carinae, often with some more strongly developed than others; scutellum flat, centrally smooth, the posterior margin sometimes granular; mesopleural disc granular to rugose; sternaulus most strongly impressed posteriorly, with 7 to 12 cross carinae superimposed on a granular background, an irregular carina sometimes developed along the posterodorsal margin; prepectal carina complete; prepectal area smooth to weakly granular; dorsal areas and sides of propodeum coarsely granular to reticulate; all propodeal carinae well developed and prominent, the basal carina about equal to its forks; areola and area petiolaris crossed by several transverse carinae; posterior-dorsal-lateral propodeal angles distinctly produced to form well developed tubercles; fore tibia with 12-16 spines in an irregular single row and a row of 6 at apex; outer apical lobe of hind tibia with a row of 3-4 rather elongate spines; hind coxae angled basally below, ventrally coarsely granular with some oblique striations dorsally; fore coxae smooth; middle coxae granular dorsally, smooth ventrally; second abscissa of radius decidedly longer than first intercubitus; subdiscoideus arising from upper half of brachial cell; tegulae smooth.

Abdomen: Petiole arched at base, longitudinally striate dorsally; gaster entirely smooth and polished except ultimate tergite which bears longitudinal striations on basal half (these usually not visible unless tergites are distended) and a granular ventral apical margin; tergite (2-3) without thickened lateral margins, but occasionally with faint aciculation at extreme base.

Color: Body color varying from uniformly testaceous (*S. dignus*) to dark ferrugineous or castaneous; in some individuals, propodeum, petiole and most of tergite (2-3) are distinctly lighter than remainder of body; legs usually concolorous with body, though in some specimens lighter, especially basal segments; tibiae not or indistinctly banded at base; clypeus, basal antennal segments and mandible bases sometimes suffused with dirty yellow; ovipositor sheath tips and apical 6-8 flagellomeres darker than respective basal portions, often brown; flagellomeres each with a narrow darker apical band; fore wing as in Figure 10, wings of males and lighter individuals approaching a subhyaline condition; costa, media and basal veins and stigma brown, remaining veins light brown or tan.

Males: Agree with females in all essential features except for the laterally thickened margin of tergite (2-3) and flagellum more slender, the first 5 flagellomeres more than 2x as long as wide; intensity of body sculpture, especially of vertex and temples, sometimes reduced; color variation also similar to that of females.

Remarks: Through the courtesy of Dr. René Béique, I have examined Provancher's type of *Rhopalophorus fasciatus** (renamed *Spathius dignus* by Muesebeck and Walkley, 1951) and see no justification for retaining it as a separate species. It agrees with the typical *S. brachyurus* in every respect except that it is a very light-colored individual, being wholly testaceous except for a darker gaster beyond tergite (2-3), but falls readily within the range of

* The lectotype of *Rhopalophorus fasciatus* bears a blue label with the handwritten number 701 and a yellow label with the printed number 1281, and a lectotype label by P. M. Marsh, Feb., 1965. The abdomen is broken off and glued to the blue label. See also Gahan and Rohwer, 1917, and Shenefelt, 1968.

color variation exhibited by the material of S. brachyurus before me. Since fasciatus is preoccupied by Walker (1874), Spathius brachyurus Ashmead becomes the oldest available name for the species, and S. dignus Muesebeck and Walkley falls as a synonym.

Following his description of S. brachyurus, Ashmead states "bred Nov. 10, 1890, and March 15, 1891, from Dryocoetes autographus living under bark of dead Abies excelsa ..." (see also Hopkins, 1892). According to the original Hopkins manuscript on file in the U. S. National Museum, specimens matching these data bear the numbers 5139 and 167 respectively. In the U. S. National Museum collection are two pins bearing the label "5139 Hopk. W. Va."* One has four specimens of S. brachyurus, each on a separate point, and a cluster of cocoons beneath on the pin. The other bears two specimens, each on a separate point. The former has two additional labels, "Spathius brachyurus Ashm. ♀" in Ashmead's writing and a red label "Type No. 2151 USNM". Of the four original specimens, one is completely gone, a second broken and the other two females in good condition. I have placed a red ink mark near the base of the point of one of the good females, and here designate this female as the lectotype. The other specimens having the number 5139 have been labeled as paralectotypes.

The number 167 is on the label of one specimen of Spathius in the U. S. National Museum collection; however, this specimen is definitely not S. brachyurus, but S. canadensis. Also in the U. S. National Museum are one female, one male, and two cocoons, all on a pin of S. brachyurus bearing the number 2442; this number is also on Hopkin's original manuscript, with the same host data except that the adults emerged April 6, 1891. Presumably Ashmead must also have had these before him when he described S. brachyurus, even though he did not specifically mention any males in his description; thus, I am designating these also as paralectotypes.

In summary, 3 pins bearing a total of 7 intact specimens (6♀♀, 1♂) are believed to have been part of the original material on which Ashmead based his description of S. brachyurus; one of these has been designated as lectotype and the others as paralectotypes.

Diagnosis: This species may be distinguished from its closest relative, S. brevipalpus, sp. n., by head shape, especially the less broad temples (Fig. 8), by the more elongate maxillary palpi, and by having the gastral setae arranged in a more or less distinct row on each tergite as opposed to the scattered arrangement in two or three rows per tergite characteristic of brevipalpus. Both may be readily separated from all other North American Spathius by the combination of propodeal tubercle, flat scutellum, polished gaster and coarsely sculptured head.

Distribution: Eastern North America north of North Carolina and Tennessee. I have seen specimens from Connecticut, Massachusetts, New Hampshire, New York, North Carolina, Ohio, Rhode Island, Tennessee, Virginia, West Virginia, Wisconsin, and Quebec, Canada. Also, in the U. S. National Museum is one broken specimen labeled from the Chiricahua Mountains of Arizona; this is possibly a labeling error.

* The Hopkins manuscript has two numbers 5139. The first is indicated as bred from a curculionid under Pinus inops bark, Sept. 28; the second bears the data cited in Ashmead's description; however, this second number was originally typed as 5189, with the 8 subsequently written over as a 3. I suspect the first 5139 should then have been changed to 5189.

Biology: Except for host records, nothing is recorded for this species. However, a cluster of 7 cocoons pinned with an equal number of adults (6♀♀, 1♂) from Branford, Connecticut (CAES), indicates that *S. brachyurus*, like *S. floridanus*, has multiple oviposition in a single host.

Hosts: Published host records for *S. brachyurus* include *Pissodes strobi* (Peck) (Curculionidae) in pine and the scolytids *Dryocoetes autographus* (Ratzeburg) in spruce and *Phloeosinus dentatus* (Say) in red cedar. A summary of the literature references to these hosts may be found in Bushing (1965). The last-named host is probably erroneous, the original record (Riley and Howard, 1890) referring to a manuscript species, *Spathius abdominalis* Riley,* and there are no later records to substantiate it. No host records were published for *S. dignus*.

The only new host record is *Pissodes approximatus* Hopkins in Scotch pine from Virginia (Hopkins No. 10099t¹). Host trees from which *S. brachyurus* has been reared include *Picea* spp., *Abies* spp. and *Pinus* spp. (mostly *strobilus*); a series of females from Wood Co., Wisconsin (RDS), is labeled from light trap.

2. *Spathius brevipalpus*, new species

(Figs. 7, 11)

Holotype. - female, North Carolina: Salisbury (J. S. Pinckney). [USNM Type No. 70498].

Description of type female: Body length, 3.3 mm; FWL, 2.2 mm; ovipositor sheath length, 1.2 mm. Other measurements and ratios in Table 1.

This species is very close to *S. brachyurus* and may be compared to it as follows:

Head: Sculpture as in *S. brachyurus*; face in profile distinctly more protuberant (Fig. 7); antennae about as long as FWL, inserted on a distinct frontal prominence; flagellomeres 19, those beyond the first subcubical, less than 2x as long as wide and lacking a corona of distinctly longer setae; eyes smaller, resulting in a longer TW and MS (see Table 1); maxillary palpi (Fig. 7) greatly reduced, total length not longer than EH; hypostomal carina highly protuberant to form a strong lip.

Thorax: Like *S. brachyurus* except as follows: lateral area of prothorax less distinctly delimited posteriorly; scutellar disc delicately granular at margins; mesopleura and sternauli uniformly very coarsely granular, sternauli lacking distinct cross carinae; fore tibia with an irregular row of about 15 spines and a row of 4 spines at apex; outer apical lobe of hind tibia with 3 spines; basal carinae of propodeum about half as long as its forks, all propodeal carinae strongly developed.

Abdomen: As in *S. brachyurus* except tergites have more setae, in two or three irregular rows per tergite, as opposed to the single obvious row per ter-

* Riley's manuscript species was never formally described and is therefore a *nomen nudum*. Indications in the Hopkins Card File in the USNM suggest that this species was conspecific with *S. brachyurus* Ashmead; this may have been the basis for its host record being transferred to that species, first by Chamberlin (1939).

gite in *S. brachyurus*; base of tergite (2-3) weakly aciculated.

Color: Body uniformly testaceous; antennae uniformly testaceous, flagellomeres lacking a darker apical band; wings hyaline (Fig. 11), no trace of a band, all veins and stigma uniformly light brown or tan (second intercubitus and intersection of recurrens, first cubitus and first intercubitus not effaced).

Variation: Paratype females. Major variation is in color, the two paratypes being more darkly pigmented than the type, the one from Raleigh, North Carolina, almost uniformly brown. The spines on the fore tibiae are difficult to see and count accurately.

Male: Unknown.

Paratypes: North Carolina: Raleigh, 1♀, 1 Sept. 1947, light (M. W. Wing) [USNM]. South Carolina: Spartansburg, 1♀, Hopk. No. 11209a³ (T. E. Snyder) [USNM].

Remarks: This unique species is readily distinguished from all other North American *Spathius* by the greatly reduced maxillary palpi which are the basis for the specific name, *brevipalpus*.

Distribution: Aside from the type material, two additional broken female specimens are in the U. S. National Museum collection, one from Durham, N. C., the other from Jacksonville, Texas. This suggests that *S. brevipalpus* probably has a range covering the southeastern United States west to Texas.

Hosts: The paratype with Hopkins No. 11209a³ was bred from "red top pine"; a list of associated insects is under this number in the Hopkins card file at the U. S. National Museum. The label on the specimen from Durham, N. C., states "ex *Pachylobius picivorus*", a curculionid, a record which should await further confirmation.

3. *Spathius marshi*, new species

(Figs. 4, 5, 9)

Holotype. - female, Maryland: Patuxent [= Patuxent] Wildlife Ref. (P. M. Marsh). [USNM Type No. 70499].

Description of type female: Body length, 3.3 mm; FWL, 2.6 mm; ovipositor sheath length, 1.8 mm. Other measurements and ratios in Table 1.

Head: Antennae slender, about 1.3x FWL; flagellomeres 22 right side, 23 left side, each with apical corona of 4 erect setae, about 2x as long as other flagellomere setae; face smooth with transversely wrinkled striations; frons smooth with delicate transverse striations centrally; vertex smooth, temples smooth, except faint raised rugosities paralleling occipital carina posteriorly; malar space smooth; occipital carina with several irregular short anteriorly directed branches laterally (Fig. 5); ocellar triangle slightly raised, smooth; eyes reduced, sparsely covered with short setae.

Thorax: Lateral area of prothorax deeply excavated, smooth and relatively broad, delimited by well defined carinae (Fig. 5); mesonotum moderately declivous, the lobes coarsely rugose with granular centers; notauli foveolate, deeply impressed and slightly lighter than mesonotal lobes; scutellar furrow deeply excavated, the anterior and posterior margins scalloped on either side of a well developed median cross carina; scutellar disc rugose; mesopleural disc smooth; sternaulus (Fig. 5) divided into two deep foveae by a strong median cross carina, a well developed longitudinal carina extending posteriorly to the mesocoxal cavity, forking about midway; prepectal carina complete; prepectal area smooth with two weak horizontal carinae; fore tibia with 24 spines

arranged in an irregular double row, a row of 5 spines at apex; hind tibiae with raised parallel longitudinal ridges below, outer apical lobes with 3 spines; fore and mid coxae smooth, hind coxae rugulose; hind tarsal segment 1 about 2.4x segment 2; second abscissa of radius distinctly longer than first intercubitus; subdiscoideus arising above middle of brachial cell; propodeal carinae all well developed, without trace of lateral branches (Fig. 4); basal carina about 1.3x the basal forks; segments of basal forks subequal on either side of costula insertion; dorsal areas and areola with reticulate surface rugosity; area petiolaris rectangular, about 3x as long as wide, subequal to the pentagonal areola in length, the carina separating them strongly protuberant and visible as a distinct toothlike projection in profile (Fig. 5); posterior-dorsal-lateral angles very weakly protuberant.

Abdomen: Petiole arched and dorsoventrally thickened at spiracles (Fig. 5), with smooth longitudinal striations dorsally; gaster smooth and shining, with no trace of surface sculpture; lateral margins of tergite (2-3) not thickened basally.

Color: Head shining orange brown, except face and malar area suffused with yellow; maxillary and labial palpi stramineous; mandibles testaceous except teeth darker; scape, pedicel and basal flagellar segments yellow brown, flagellum becoming gradually light brown apically; thorax, propodeum, petiole and gaster ferrugineous except prothorax which is testaceous; gaster shining, the tergites with ill-defined subapical, subcuticular testaceous bands; legs yellow brown except ferrugineous hind femora, tibiae not or indistinctly banded at base; wings (Fig. 9) subhyaline, costa and basal third of stigma tan, other veins and remainder of stigma medium brown; tegulae testaceous, shining; ovipositor sheaths yellow brown basally, becoming gradually brown toward apex.

Variation: Paratype females. In addition to characters given in Table 1, minor variations in number and development of the cross carinae of the scutellar furrow, sternauli and area petiolaris occur, with up to 4 distinct scutellar carinae and the sternauli either undivided or comprised of as many as 4 foveae. The number of fore tibial spines varies from 17 to 26. The Maine paratype differs from the others as follows: the sternauli are merely deep depressions without thickened margins (hence not true foveae) and the carina extending from the posterior margin to the mesocoxal cavity is totally effaced on the anterior half; the prepectal carina is incomplete medially and there are additional short horizontal carinae immediately above the prepectal area, which has in addition a medial vertical carina; instead of delicate transverse striae, the frons has delicate irregular raised rugosities medially; the petiole arches distinctly beyond the spiracles at about its geometric midpoint; the carina between the area petiolaris and areola is not protuberant and the forks of the basal carina are distinctly arched instead of straight. While these differences may prove to merit specific designation, I chose to include it here until more material is available.

Paratype males: The two known males agree with the holotype in color and sculpture, except they have the frons smooth, the petiole more slender and elongate, and one from Virginia lacks median cross carinae on the sternauli.

Paratypes: 1♀, same data as holotype [USNM]. Iowa: Mt. Pleasant, 1♀, 26 May 1934 [USNM]. Kansas: Onaga, 1♀, 2 June 1923 (Crevecoeur) [KSU]. Maine: Round Mt., 1♀, 16 July [MCZ]. Maryland: nr. Colesville, 1♀, 28 May 1914 (R. C. Shannon) [USNM]; Beltsville, 1♀, April 1941 (A. E. Davis) [USNM]. Michigan: Ann Arbor, 1♀, 29 May 1962 (H. & M. Townes) [Townes]; St. Joseph Co., 1♀, 5 Aug. 1953 (R. R. Dreisbach) [Townes]; Wayne Co., Grosse Isle, 1♀, 13 Aug. 1956 (G. Steyskal) [Townes]. New York: Chappagua,

1♀, 18 May 1937 (L. L. Pechuman) [USNM]. Pennsylvania: Stoverdale, 1♀, 25 Aug. 1916 (W. S. Fisher) [USNM]. Tennessee: Chapin Sanctuary, East Ridge, 1♂, 9 May 1952 (O. Peck) [CNC]. Virginia: Arlington, 1♂, 8 Sept. 1952 (K. V. Krombein) [USNM].

Remarks: This species may be distinguished from all other North American *Spathius* by the smooth mesopleural disc and the rugose scutellum and mesonotal lobes. The unique form of the sternauli, lack of banded wings, and propodeal profile (Fig. 5) are also useful diagnostic characters. Interestingly, a very similar propodeal profile also occurs in *S. cassidoris* Nixon from New Guinea (Nixon, 1943, p. 268). This distinctive species is named for its collector, Dr. Paul M. Marsh, in grateful appreciation for his continued interest and encouragement throughout this study.

Distribution: The localities of the paratypes indicate that the range of *S. marshi* is apparently eastern North America north of Virginia and Tennessee and west to Iowa. In addition to the paratypes, I have seen specimens from Illinois and Quebec, Canada.

Host: No hosts are known. The New York paratype is labeled from apple, and that from Pennsylvania from hickory.

4. *Spathius stigmatus*, new species

(Figs. 6, 12, 13)

Holotype: - female, New York: Ithaca, 17 Aug. 1947 [CNC].

Description of type female: Body length, 4.4 mm; FWL, 2.9 mm; ovipositor sheath length, 7.5 mm. Other measurements and ratios in Table 1.

Head: Antennae short, about equal to FWL; flagellomeres 18, subcubical, those beyond the third less than 2x as long as wide; flagellomeres each with a corona of 4 evenly spaced erect elongate setae about 4x as long as other flagellar setae (Fig. 6); face transversely striate; frons centrally delicately transversely striate, becoming faintly granular toward eyes and antennal bases; vertex adjacent to ocellar triangle smooth, posteriorly becoming delicately transversely striate, this continuing laterally onto temples to malar space; mandibles striate basally below, the tips dark; ocellar triangle weakly raised, appearing smooth; maxillary palpi slightly reduced, extending to about posterior border of forecoxae, the segments laterally compressed and gently curved, the apparent second longer than any other segment.

Thorax: Lateral area of prothorax narrow and poorly defined; propleura horizontally carinate; mesonotum moderately declivous, the lobes evenly granular; notauli deeply impressed anteriorly, converging to a broad, slightly depressed longitudinally rugose area; scutellar furrow with about 10 evenly spaced cross carinae; scutellum trapezoidal, about as long as basal width and slightly convex, its disc uniformly granular, becoming weakly rugose posteriorly; mesopleural disc finely horizontally strigose; sternaulus shallow, crossed by about 10 moderately developed carinae, these continuing posteriodorsally onto mesopleural disc; prepectal carina complete; prepectal area with irregular surface rugosities and about 4 to 6 short horizontal carinae arising along anterior margin and extending posteriorly about to middle of area; propodeal carinae basad of costulae obscured, entire dorsal area uniformly granular, becoming rugose-reticulate apically; dorsal and lateral carinae well developed, as are those enclosing the almost square area petiolaris; posterior-dorsal propodeal angles weakly protuberant; tegulae delicately shagreened; fore tibia with 13

spines arranged in an irregular single row, a row of 6 spines at apex; outer apical lobe of hind tibia with a row of 4 rather stout spines; hind coxae angled basally below; hind tarsi shorter than hind tibiae, the basitarsi about 2.3x as long as the second tarsomeres; second abscissa of radius about 1.8x first intercubitus; recurrens about equal to first abscissa of radius; subdiscoideus nearly interstitial.

Abdomen: Petiole slightly arched at base, about equal in length to tergite (2-3); petiole sculpture dorsally granular except finely longitudinally striate on apical $1/4$ with a pair of longitudinal dorsal carinae along each side; tergite (2-3) smooth except for fine aciculation at extreme base, the lateral margin weakly thickened at base; remainder of gaster appearing uniformly delicately shagreened, strongest on epipleurites; ultimate tergite with fine basal longitudinal striations (not visible unless tergites are distended).

Color: Head, thorax, propodeum, legs and petiole ferrugineous; gaster castaneous, lighter at apex ventrally; maxillary and labial palpi light brown; antennae light ferrugineous, the apical 6-8 flagellomeres becoming brown and all flagellomeres with a narrow darker apical band; tibiae lightened on about basal $1/4$, appearing banded, this most apparent on hind tibiae; wings (Fig. 12) infumated except subhyaline tips and a transverse band from the stigma base; veins and stigma (except base) light brown; ovipositor sheaths ferrugineous, the tips dark brown.

Variation: Paratype females. Gaster color in 2 females is completely light ferrugineous. In others, tergite (2-3) is all or in part ferrugineous, the remainder of the gaster being castaneous. The lighter specimens also show a reduction in wing and leg band intensity. In about half of the paratypes, the subdiscoideus is exactly interstitial. In sculpture, basal aciculation of tergite (2-3) covers as much as the basal $1/3$ of the tergite in some specimens and carinae development on the prepectal area may be reduced or sometimes entirely absent. Number of scutellar furrow carinae varies from 10 to 15, and number of fore tibial spines from 12 to 15. Variation in measurements and ratios is given in Table 1.

Paratype males: The five male paratypes agree with the females in all important respects except the hind wings show distinct stigmal development (Fig. 13) and the margin of tergite (2-3) is thickened for $2/3$ of its length.

Paratypes: 2♀♀, 1♂, same data as holotype [CNC]. Delaware: New Castle Co., 2♀♀, 5 & 7 June 1922 (F. M. Jones) [Townes]. Illinois: Urbana, 1♀, 12 July 1920 (C. P. A.) [INHS]; Elsah, Jersey Co., Principia College, 1♀, 27 April 1943 (C. L. Remington) [USNM]. Maryland: Forest Glen, 1♀, 26 Apr. 1914 (O. Heidemann) [USNM]. Michigan: Livingston Co., G. Res., 1♀, 28 May 1944 (R. R. Dreisbach) [RDS]. New York: Syracuse, 2♀♀, 2♂♂, 21 Mar. & 26 May 1916, N. Y. S. Coll. For. Lot Nos. H295, H438 (M. W. Blackman and H. H. Stage) [Syracuse, Hamden]. North Carolina: Tryon, 3♀♀, Hopk. No. 3605c and 1464f (W. F. Fiske) [USNM]. Ohio: Wayne Co., 1♀, 2 July 1941 [OSU]. Pennsylvania: Hopk. No. 10383 (Linglestown), 7♀♀, 25 June 1914 (H. B. Kirk) [USNM, MCZ]. Texas: Hopk. No. 3861 (Montell), 1♂, April 1907 [USNM]. Virginia: E. Falls Church, 1♀, 9 May 1909 (H. L. Viereck) [USNM]. Wisconsin: Gay Mills, 1♀, 8 July 1953 (C. L. Fluke) [RDS]. Canada: Hull (Quebec), 1♀, 19 Aug. 1894, 1♂, 23 June 1895 [CNC]; Ontario, Ottawa, 1♀ [USNM].

Remarks: The very long ovipositor, shagreened gaster and form of the flagellomeres (Fig. 6) readily distinguish the females. Presence of a stigma in the male hind wing (Fig. 13) will separate the males from all other known North American *Spathius*, and is the basis for the specific name, stigmatus.

Table 1. Measurements and ratios of selected characters for females of the brachyurus species group. Top line in each instance gives range; number below is for holotype or lectotype.

	<u>brachyurus</u>	<u>brevipalpus</u>	<u>marshi</u>	<u>stigmatus</u>
n	25	3	13	13
number of flagellomeres	19-25 broken	19-20 19	20-24 22, 23	16-20 18
body length (mm)	3.0-5.3 3.3	3.3-4.3 3.3	2.8-4.0 3.5	3.3-5.1 4.4
FWL (mm)	2.3-3.4 2.4	2.2-2.7 2.2	2.2-2.7 2.6	2.4-3.1 2.9
MS/EH	0.67-0.82 0.67	0.73-1.00 0.95	0.78-1.00 1.00	0.70-0.96 0.88
TW/EH	0.76-1.04 0.76	1.00-1.30 1.26	1.00-1.18 1.17	1.04-1.23 1.08
IOD/EH	1.12-1.78 1.48	1.58-1.95 1.90	1.50-1.89 1.89	1.33-1.58 1.36
OTW/OED	0.63-0.92 0.79	0.53-0.65 0.56	0.53-0.72 0.56	0.56-0.69 0.59
OED/OOD	0.68-0.90 0.88	0.82-0.83 0.82	0.82-0.95 0.90	0.67-0.80 0.71
Pet. L/(2-3)L	1.03-1.29 1.17	1.04-1.07 1.04	1.00-1.50 1.25	0.90-1.22 1.00
ICu ₁ /R ₂	0.66-1.00 0.74	0.58-0.67 0.58	0.77-0.96 0.78	0.50-0.80 0.56
OSL/FWL	0.39-0.60 0.46	0.52-0.55 0.55	0.69-0.96 0.73	2.20-2.70 2.60

In Ashmead's (1893) key, S. stigmatus keys out exactly to S. laflammei Provancher, and indeed one specimen from CNC bears this determination label in Ashmead's handwriting.

Distribution: Paratype localities suggest a distribution covering eastern North America, although except for Texas the species has not been recorded south of North Carolina. Additional specimens add only Indiana.

Hosts: Hopkins cards in the U. S. National Museum and records of Blackman and Stage (Syracuse) indicate that S. stigmatus has been reared from hickory dead 3-4 years in association with the cerambycid Neichnea laticornis Say and the clerid Phyllobaenus dislocatus Say (from Hopk. No. 10383). Black-

man and Stage's (1924, p. 165) reference to *Spathius trifasciatus* Riley is probably a misidentification and instead almost surely refers to this new species, since the data on the specimens is in almost exact agreement. They conclude that one of its hosts is *Magdalis olyntha* Herbst. (See also "Hosts" and "Remarks" under *S. trifasciatus*.) The paratype from Texas was reared from pecan infested by cerambycids which had previously emerged; several associated insects are listed under Hopkins No. 3861. Of two additional females in the U. S. National Museum, one was reared from *Celtis* (Hopk. No. 2573) and the other bears the label "parasitic on *Xyloterinus politus* [Scolytidae] in maple."

5. *Spathius calligaster*, new species

(Figs. 17, 20)

Holotype. - female, South Carolina: Georgetown, 28 Mar. 1938 (F. C. Craighead) ex. *Melasis pectinicornis* ? in Myrtle [USNM Type No. 70500].

Description of type female: Body length, 5.6 mm; FWL, 3.7 mm; ovipositor length, 5.5 mm.* Other measurements and ratios in Table 2.

Head: Head slightly dorsoventrally compressed (Fig. 17), the eyes slanted obliquely, creating a relatively broader lower temple area; flagellomeres 37; face transversely strigose-granular; frons transversely striate, the center area slightly rugose; vertex delicately transversely striate anteriorly, posteriorly becoming smooth in front of occipital carina; temples delicately strigose more or less parallel to occipital carina, this strongest posteriorly, becoming smooth at eye and malar space; ocellar triangle very weakly raised and delicately granular, areas between the lateral ocelli and eyes, separating vertex and frons, smooth.

Thorax: Thorax strongly dorsoventrally compressed (Fig. 17), about 3x as long as high at tegulae; lateral areas of prothorax distinct and moderately excavated, the anterior margins converging dorsally to form a distinct transverse swelling slightly in front of the anterior mesonotal margin (Fig. 17); notauli crenulate anteriorly, meeting in a broad slightly depressed rugose area; mesonotum sloping gradually to pronotum, the lobes evenly granular; scutellar furrow shallow, narrowest medially, about as wide as distance between lateral ocelli and crossed by about 7 variously developed carinae, some partially obscured; scutellum nearly flat and evenly granular on disc; mesopleural disc nearly smooth immediately above sternaulus, becoming delicately horizontally strigose to reticulate-rugose on upper portions and granular posteriorly; sternaulus moderately excavated, a gently curved furrow, deepest about midway between fore and middle coxae and with several irregular raised cross carinae which do not continue onto mesopleural disc; prepectal carina incomplete dorsally above sternaulus (Fig. 17); prepectal area smooth and somewhat reflexed posteriorly, with a few hairs and faint irregular raised rugosities; propodeum nearly horizontal; propodeal carinae mostly obscured, lateral carinae best developed; areola, costulae and basal forks completely obscured by reticulate rugosity which merges into the coarsely granular dorsal areas; basal carina faintly developed, rather long, extending to about half

* In this species the ovipositor sheaths tend to coil strongly on all dried specimens, hence the actual ovipositor length was measured.

the length of propodeum; fore tibia with 19 spines arranged in an irregular double row and with a row of 7 spines at apex; outer apical lobe of hind tibia with no spines present; hind coxae elongate, slender and coarsely granular all over, except for very faint oblique striation dorsally; outer face of hind tibiae irregularly longitudinally striate; tegulae granular medially, the outer portions smooth; subdiscoideus vein exactly interstitial; first abscissa of radius distinctly shorter than recurrens; first intercubitus with a distinct curvature (Fig. 20); mediella with 3 distinct abscissae.

Table 2. Measurements and ratios of selected characters for females of the calligaster and longipetiolatus species groups. Top line in each instance gives range; number below is for holotype or lectotype; longipetiolatus is known only from the type.

	<u>calligaster</u>	<u>longipetiolatus</u> (holotype male)	<u>elegans</u>	<u>evansi</u>
n	12	1	16	11
number of flagellomeres	27-42 37	22	30-39 31	35-48 45
body length (mm)	3.5-6.5 5.7	3.4	3.4-6.8 5.6	3.7-8.5 6.4
FWL(mm)	2.5-4.5 3.7	2.4	2.7-5.0 4.2	3.2-5.5 4.7
MS/EH	0.48-0.57 0.57	0.43	0.49-0.65 0.49	0.48-0.60 0.50
TW/EH	0.68-0.94 0.71	0.57	0.62-0.78 0.67	0.57-0.69 0.63
IOD/EH	1.13-1.35 1.20	1.14	1.05-1.28 1.05	1.02-1.14 1.08
OTW/OED	0.59-0.75 0.67	1.00	0.68-0.89 0.83	0.70-0.85 0.72
OED/OOD	0.77-1.00 0.83	0.67	0.63-0.79 0.72	0.63-0.72 0.67
Pet. L/(2-3)L	1.04-1.24 1.23	1.40	1.55-1.89 1.89	1.45-1.71 1.53
ICu ₁ /R ₂	0.83-1.00 0.91	0.96	0.81-1.33 1.08	0.88-1.12 1.05
OSL/FWL	1.28-1.71 1.48	-	1.06-1.51 1.43	1.58-2.02 2.02

Abdomen: Petiole straight, not arched basally, sculpture coarsely granular to rugose reticulate with a pair of wrinkled longitudinal carinae along most of each side above the spiracles; tergite (2-3) entirely coarsely granular-reticular except apical margin which is smooth, the sculpture strongest on basal half, this delimited by a faint transverse line at about midpoint of tergite; tergite (2-3) thickened laterally almost entire length; remaining tergites granular basally, the apical margins distad of the setae rows smooth; intensity of sculpture progressively diminishes on each succeeding tergite, becoming punctulate on penultimate tergite; epipleurites lacking obvious sculpture, at most dull shagreened.

Color: Body color more or less uniformly pale testaceous except the posterior margin of the mesonotum and scutellar carinae are dark brown and gaster with very faint darker subcuticular transverse bands dorsally and pale stramineous ventrally; antennae, tegulae and fore legs honey yellow; maxillary and labial palpi, all trochanters, basal $1/4$ to $1/3$ of tibiae, and fore and mid coxae cream white; hind coxae, mid and hind femora and tibiae darker, dull testaceous; mandible tips ferrugineous; ovipositor sheaths pale testaceous, the tips darker, almost brown; wings banded as in Figure 20; costal vein honey yellow, other veins tan, the basal vein and media darkest; basal $1/3$ of stigma pale stramineous.

Variation: Paratype females. In addition to variation indicated in Table 2, body color may be generally darker to more or less uniformly dull ferrugineous; however, the basic pattern prevails, i.e., the fore and mid coxae are always much lighter than the hind coxae, and the antennae, fore legs and tegulae are usually at least slightly lighter than the predominating body color; flagellomeres, at least basal ones, often with a darker narrow apical rim; eyes gray to black, very rarely showing any iridescence in white light; prepectal carinae variously developed, almost completely obscured in the smallest female and occasionally appearing complete in larger individuals; subdiscoideous position somewhat variable, not always interstitial; gastral sculpture beyond tergite 4 varying in degree of development, usually much diminished in intensity, the apical tergites often nearly smooth; number of fore tibial spines varying from 14-22, with a row of 6 or 7 at apex.

Paratype males: In general variation in the males parallels that found in females. Additionally, males often have some tergites beyond (2-3) laterally thickened, and also the hind wings show a slight tendency towards stigma development.

Paratypes: 12♀♀, 7♂♂, same data as holotype [USNM]. Canada, Quebec: La Trappe, 3♀♀, 1♂, 20 July 1947, 27 July 1948, 12 July 1950, 3 Aug. 1943 (J. Ouellet) [Montreal, CNC, MCZ]. U.S.A., Illinois: White Heath, 2♀♀, 2 Aug. 1940 (Ross & Riegel) [INHS]. Maryland: Patuxent Wildlife Ref., 1♂ (P. M. Marsh) [USNM]. New Jersey: Metuchen, 1♂, 13 June 1964 (Porter) [Porter]; Moorestown, 1♂, 1♀, 23 June and 13 Aug. 1939 (H. & M. Townes) [Townes]. North Carolina: Tryon, 1♀, 10 May 1946 (M. Townes) [Townes]. Virginia: Plimmers Id., 1♂, 1♀, 6 June 1916, reared from *Carpinus caroliniana*, Hopkins No. 14023 (H. S. Barber & T. E. Snyder) [USNM].

Remarks: In addition to its somewhat dorsoventrally compressed body (Fig. 17), this species may be distinguished from all other North American *Spathius* by the combination of the coarsely sculptured gaster, especially tergites (2-3) and 4, the thickened lateral margin of tergite (2-3) for most of its entire length, the absence of spines on the outer apical lobe of the hind tibia, the dorsal transverse swelling on the prothorax and the first abscissa of the radius distinctly shorter than the recurrent vein. In addition, the petiole is

straight and the subdiscoideus vein is usually more or less interstitial. In its characters this species resembles those of Nixon's labdacus group.

Distribution: The known range corresponds with the paratype localities which are scattered through the eastern United States and Quebec, Canada, including Illinois, Maryland, New Jersey, North Carolina, South Carolina and Virginia.

Hosts: The holotype series from Georgetown, South Carolina, was reared with the eucnemid, Melasis pectinicornis Melsh. in myrtle, according to their labels and data filed under Hopkins No. 17412e in the U. S. National Museum. No other associated insects are mentioned. The paratypes from Virginia were reared from Carpinus caroliniana in association with Leptura mutabilis Newm., Leptostylus macula Say (both Cerambycidae) and Melasis pectinicornis, according to data filed under Hopkins No. 14023 in the U. S. National Museum.

6. Spathius longipetiolatus Ashmead

(Fig. 22)

Spathius longipetiolatus Ashmead 1893, Can. Ent. 25: 70.

[Type locality: Florida: Jacksonville (Lectotype male in USNM, Type No. 52647)].

Redescription of lectotype male: Body length, 3.4 mm; FWL, 2.4 mm; other measurements and ratios in Table 2.

Head: Flagellomeres 22; face transversely strigose; frons with several polished transverse striations; vertex strongly transversely striate like frons, those of vertex separated from those of frons by a smooth transverse space about width of ocellar triangle, the striae nearly obscured medially; temples smooth and shining; ocellar triangle slightly raised, polished.

Thorax: Lateral areas of prothorax broad, deeply excavated and polished, bordered by a well defined carina and crossed by 7-8 oblique carinae; notauli shallowly crenulate anteriorly, meeting in an area of weak rugosity from which emerge 2 posterior carinae extending to posterior margin of mesonotum; mesonotum abruptly declivous, the lobes evenly granular; scutellar furrow with 3 prominent cross carinae flanked laterally by a less strong carina on each side; scutellum slightly projecting and more or less smooth, with faint sculpture laterally and posteriorly; mesopleural disc smooth and shining above sternaulus, becoming somewhat rugose dorsally; sternaulus deeply excavated, especially posteriorly, smooth, crossed by 6 or 7 carinae, the space posterior to furrow with curved striae extending to mesocoxal cavity; prepectal carina complete; prepectal area smooth with slight surface irregularity; propodeal carinae all distinct; basal carina about $1/4x$ as long as its forks; fore tibia with at least 12 spines arranged in a single row; outer apical lobe of hind tibia with apparently 4 spines; tegulae smooth; subdiscoideus vein nearly interstitial; recurrent vein almost $2x$ first abscissa of radius; first intercubitus and second abscissa of radius subequal.

Abdomen: Petiole slender and elongate, about $2/3$ as long as thorax and irregularly longitudinally strigose dorsally; tergite (2-3) nearly smooth and shining, very faintly shagreened at base; remaining tergites smooth and shining, the lateral margins thickened; genitalia as in Figure 22.

Color: Body color light ferrugineous, the head lighter testaceous and petiole darker, almost castaneous; antennae testaceous on basal segments, becoming gradually darker apically; legs unicolorous, honey yellow, the tibiae

not banded and the tarsi very slightly darker; maxillary and labial palpi and tegulae testaceous; propodeal spiracle testaceous, contrasting with ferrugineous propodeum; wings subhyaline, the veins light yellowish-brown; stigma wholly brown, very slightly lighter basally.

Variation: Paralectotype male. Agrees with type in all apparent respects, but its poor condition makes adequate comparison impossible.

Female: Unknown.

Remarks: Since its description, no additional collections or records of this species have been made, and the two males on which this species is based remain unique among the Nearctic species. The combination of the smooth scutellum, slender elongated petiole, strong transverse striation on the vertex and deeply excavated sternauli and lateral areas of the prothorax make this a very distinctive species and I found no specimens which possessed these features among the material studied. The elongate petiole most resembles that of *Spathius elegans*, sp. n., but the two differ strikingly in most other features.

As was true for several of the *Spathius* described in his 1893 paper, Ashmead gave no formal description of *S. longipetiolatus* beyond the characters used in his "Table of Species". Although not specifically stated by Ashmead, there seems little doubt that he had at least two males before him, since he states a range for the length of "2.5-3.0 mm". In the U. S. National Museum collection are two males bearing three identical labels: "Jacksonville, Fla.", "*Spathius longipetiolatus* Ashm." in Ashmead's handwriting, and red "USNM Type No. 52647" on one and "USNM Paratype No. 52647" on the other. Both specimens were very dirty and embedded in glue; one I cleaned, extracted the genitalia, remounted, and have designated as lectotype. The other (missing the wings and abdomen) I labeled as paralectotype without attempting to clean it.

Distribution: Known only from the type locality, Jacksonville, Florida.

Host: Unknown.

7. *Spathius elegans*, new species

(Fig. 22)

Holotype.- female, Maryland: Plummers Id., vi-6-13, reared *Acer*, Hopkins No. 11338 (H. S. Barber) [USNM Type No. 70501.]

Description of type female: Body length, 5.6 mm; FWL, 4.2 mm; ovipositor sheath length, 6.0 mm. Other measurements and ratios in Table 2.

Head: Flagellomeres 31; face finely transversely strigose-granular, becoming granular at eyes; frons strongly transversely striate, this ending abruptly at level of lateral ocelli; vertex smooth and shining, no trace of any sculpture; temples mostly smooth and shining, a very faint trace of delicate vertical strigosity next to occiput, but perfectly smooth at eye and malar space; ocellar triangle weakly raised with weak central sculpture.

Thorax: Lateral areas of prothorax relatively broad and well defined anteriorly with prominent diagonal cross carinae, posteriorly becoming obscured in the irregular granular rugosity which covers most of propleura; pronotum with a well developed transverse ridge just behind the anterior margin; notauli crenulate anteriorly, converging into a broad moderately depressed rugose area; mesonotum moderately declivous, the lobes more or less evenly granular; scutellar furrow deep, with about 4 well developed cross carinae; scutellum very slightly convex and projecting, the disc granular, becoming

weakly rugose posteriorly; mesopleural disc irregularly rugose to granular; sternaulus a distinct furrow extending about $2/3$ of mesopleuron, with several irregular to almost rugose cross-carinae; prepectal carina complete, well developed; prepectal area smooth, shining, with a weak horizontal carina just above the fore coxa; propodeal carinae all visible, tending to be somewhat irregular and wrinkled; dorsal areas coarsely granular to weakly rugose; basal carina quite well developed, straight and about equal in length to its less well developed forks; areola and area petiolaris rather narrow and elongate, the sides subparallel, weakly rugose basally, the rugosity stronger apically; fore tibia with 39 spines arranged in row of 2-3 with an irregular row of 9 at apex; outer apical lobe of hind tibia with a row of 4 spines; hind basitarsus distinctly longer than second tarsomere (ratio of $32/13$) and tarsomere 3 slightly shorter than tarsomere 5; subdiscoideus not interstitial; second abscissa of radius slightly shorter than first intercubitus; mediella with 3 abscissae.

Abdomen: Petiole slender and nearly straight, about $3/4$ as long as thorax (Fig. 22), granular to weakly rugose dorsally, becoming irregularly longitudinally striate apically; tergite (2-3) with basal $3/8$ prominently longitudinally strigose-granular, abruptly delimited apically, followed by equal area of delicate scaly-reticulation grading imperceptibly into apical $1/4$ which is smooth and shining; lateral margin of tergite (2-3) thickened on about basal $3/8$; tergite 4 with faint sparse punctulation anterior to the setae row; remaining tergites apparently smooth.

Color: Head, pro- and mesothorax testaceous; propodeum and petiole honey yellow, distinctly lighter than remainder of thorax or gaster; gaster shining ferrugineous except for a honey yellow transverse band on apical $1/4$ of tergite (2-3); legs more or less concolorous with head and thorax, except for stramineous trochanters, fore and mid coxae and basal $1/4$ to $1/5$ of tibiae; palpi also stramineous; antennae honey yellow basally becoming progressively darker testaceous towards apex; fore wing distinctly banded, the basal third of stigma whitish; veins testaceous to brown; eyes dark gray.

Variation: Paratype females. Considerable variation in size, color and intensity of sculpture occurs; color is most commonly dull ferrugineous, but varies from testaceous to mostly piceous; however, the pattern always remains, especially having the propodeum and petiole distinctly lighter than the remainder of the thorax and gaster, even to the naked eye; the lighter transverse band on the apical margin of tergite (2-3) is usually discernible on the majority of individuals, but may occasionally be obscured, the gaster appearing unicolorous; eyes never with iridescent hue in white light; intensity and development of the striation on the frons varies greatly, smaller examples tending to have almost smooth frons; the vertex, however, is always smooth and shining; sculpture on the basal $3/8$ of tergite (2-3) is always distinctly present, but that on the next $3/8$ is variable, sometimes almost completely obscured; the rugose sculpture of the mesopleuron is also variously expressed, occasionally obscured; scutellar furrow with 3-8 variously developed cross carinae, some of which may be wrinkled and irregular medially; relative lengths of the first intercubitus and second abscissa of the radius are not reliable, about half of the individuals having the first intercubitus shorter than or equal to the second abscissa of radius; hind basitarsus is always distinctly longer than the second tarsomere and the fifth tarsomere is usually slightly longer than the third; number of fore tibial spines varies from 22-48 with a row of 7-10 at apex; outer apical lobes of hind tibiae with a row of 3-5 spines. Variation in measurements and ratios given in Table 2.

Paratype males: In general, variation tends to parallel that in females.

Smaller males are very difficult to distinguish because the useful sculpture differences tend to become obscured.

Paratypes: 6♀♀, same data as holotype [USNM]. Canada, Ontario: Pt. Pelee, 1♀, 1 July 1957 (H. & M. Townes) [Townes]; Ottawa, 1♀, 16 Aug. 1947 (W. R. M. Mason) [CNC]. Quebec: Messines, 1♀, 10 July 1947 (W. R. M. Mason) [CNC]; Wakefield, 1♀, 20 June 1946 (G. S. Walley) [CNC]; Gatineau Park, Old Chelsea, 3♀♀, 8 July 1966 (D. R. Smith) [USNM]. U.S.A., Alabama: Chambers Co., Langdale, 1♀ (H. H. Smith) [USNM]. Connecticut: Redding, 1♀, 28 July 1933 (Melander) [MCZ]. Florida: Gainesville, 1♀, 19 May 1918 (C. J. Drake) [Syracuse]. Illinois: Urbana, U. of Ill. Woods, 2♀♀, 12 July and 22 Aug. 1937 (Sarah Jones) [INHS]; Jonesboro, 1♀, 21 June 1939 (Burks & Riegel) [INHS]; Warren, 1♀, 13 June 1955 (R. L. Fischer) [MSU]. Kansas: Douglas Co., 1♀, 30 May 1951 (J. G. Rozen) [Berkeley]. Kentucky: Golden Pond, 1♀, 10 June-10 Aug. 1964 (S. G. Breeland) [Townes]. Maryland: Takoma Pk., 1♂, 2♀♀, 5 July 1942, 9 May & 10 July 1943 (G. F. Townes and H. & M. Townes) [Townes]; Bowie, 2♂♂, 24 June 1945 (H. & M. Townes) [Townes]. Massachusetts: Sharon, 1♀, 3 Aug. 1904 [MCZ]; Petersham, 1♀, 17 July [MCZ]. Michigan: Midland Co., 1♀, 7 Sept. 1944 (R. R. Dreisbach) [USNM]. New Hampshire: Mt. Madison, 1♀, 24 June 1938 (H. & M. Townes) [Townes]; White Mts., Dolly Copp, 2♀♀, 13 July 1931 (A. L. Melander) [MCZ]. New Jersey: Metuchen, Woodwild Pk., 3♀♀, 6 Sept. 1955, 15 Aug. 1956, 8 July 1955 [Porter]. New York: Bemus Pt., 5♀♀, 2♂♂, 26 June and 6, 8, 11, 22, 31 July 1937 (H. K. Townes) [Townes]; Millwood, 3♀♀, 1♂, 21 June 1936 (H. K. Townes) [Townes]; Colden, 1♀, 7 June 1908 (M. C. Van Duzee) [CAS]; Albany Co. nr. Rensselaerville, Huyck Preserve, 2♀♀, 28 June and 1 July 1967 (R. & J. Matthews) [MCZ]. North Carolina: Pisgah Mt., 1♀, 21 June 1940, 4800-5300 feet (H. & M. Townes) [Townes]; Crabtree Mds., Yancey Co., 1♀, 21 Aug. 1950, 3600 ft. (H., M. & D. Townes) [Townes]. Pennsylvania: Wilawanna, 2♀♀, 25 July 1938 (R. H. Crandall) [Arizona]. Tennessee: Green Briar Cove, Mount trail, GSMN Park, 1♀, 12 June 1946 [RDS]. Vermont: Jacksonville, Laurel Lake, 1♀, 15 July 1939 (H. D. Pratt) [Minnesota]. District of Columbia: Washington, 3♀♀, 26 & 29 Aug. 1907, 7 Sept. 1907, bred from Carpinus americanus (J. A. Hyslop) [USNM].

Remarks: This is one of the most frequently collected *Spathius* species although it has so far only rarely been reared. I have seen in excess of 200 specimens. A highly variable species, it may be readily identified by the combination of the smooth, shining vertex, rugose mesopleura, long hind basitarsus (always greater than 2x the second tarsomere) and the distinctly lighter colored propodeum and petiole. A number of strongly dorsoventrally compressed individuals of *S. elegans* were also noted; these are sometimes so greatly distorted that certain identification is difficult.

Distribution: Throughout eastern North America. In addition to the paratypes, I have seen specimens from Georgia, Iowa, Maine, Mississippi, Nebraska, Rhode Island, South Carolina, Virginia, West Virginia and Wisconsin. I also tentatively include here a single female from San Juan Island, Washington (RDS).

Hosts: No positive host associations are known. The holotype series was reared from maple under Hopkins No. 11338, but no host associations were made. Two males from Plummers Island, Maryland, in the U. S. National Museum were reared from Acer under Hopkins Nos. 10178 and 11341; another male was reared from black walnut, according to Hopkins No. 2566. The paratypes from Washington, D. C., were reared from Carpinus (blue beech) and another individual I saw was reared from hickory. A teneral male, probably

of this species, was reared from powderposted wood, probably as a parasite of the anobiid Hadrobregmus, according to Hopkins No. 34373c. Brues' (1927) record of Spathius simillimus is a misidentification and should be changed to this species, as his single female reared July 17 is in the MCZ (paratype from Petersham, Mass.).

8. Spathius evansi, new species

(Fig. 21)

Holotype. - female, Wyoming: Moran, Jackson Hole Bio. Sta., Aug. 1-14, 1961, 6750 feet elev. (H. E. Evans) [MCZ Type No. 31700].

Description of type female: Body length, 6.4 mm; FWL, 4.7 mm; ovipositor sheath length, 9.5 mm.

Head: Flagellomeres 45; face transversely strigose granular; frons strongly transversely striate, becoming delicately granular at eyes; vertex very faintly transversely strigose to scaly reticulate anteriorly becoming smooth posteriorly at occiput; temples posteriorly strigose more or less parallel to occipital carina, quickly diminishing in intensity towards eye, malar space and vertex; ocellar triangle slightly raised and appearing granular.

Thorax: Lateral areas of prothorax moderately developed, smooth, crossed by several diagonal carinae, these becoming obscured posteriorly in the granular to horizontally strigose sculpture of remainder of propleura; notauli deep and crenulate anteriorly, meeting in a broad strongly depressed rugose area, dominated by two wrinkled longitudinal carinae which end at posterior margin of mesonotum; mesonotum moderately declivous, the lobes evenly granular, the median lobe with a weak longitudinal depression medially; scutellar furrow relatively broad, wider than the space between the lateral ocelli, and crossed by 9 more or less parallel carinae of which the center one is most strongly developed; scutellum slightly raised and projecting posteriorly, the disc evenly granular; mesopleural disc coarsely granular to granular-rugose dorsally; sternaulus a relatively broad, distinct furrow about $2/3$ length of mesopleuron and crossed by about 13 more or less parallel vertical carinae; prepectal carina strongly developed, especially ventrally, but almost obscured just above sternaulus; prepectal area faintly scaly-reticulate; mesosternum evenly granular, except rugose midventral line; propodeal carinae tending to be obscured except those surrounding the area petiolaris and the lateral carinae; basal carina irregularly wrinkled, about 1.2x its forks which are also irregularly wrinkled; costulae nearly obscured by weak rugosity; dorsal areas granular; areola with weak granular rugosity over basal half, apically with 3 weak short longitudinal carinae; area petiolaris smooth, about as long as broad; fore tibia with 25 spines arranged in an irregular double row and a row of 6 spines at apex; outer apical lobe of hind tibia with 2 or 3 inconspicuous spines; hind coxae elongate and uniformly scaly-reticulate to finely granular with no evidence of oblique striations dorsally; hind tarsomere 3 about 1.4x as long as tarsomere 5; tegulae with inner halves granular, outer halves smooth; subdiscoideus vein not interstitial.

Abdomen: Petiole straight, slender and nearly as long as thorax, coarsely granular dorsally with irregular longitudinal striation apically; tergite (2-3) with prominent sculpture dorsally on basal $4/5$ as follows - basal $1/2$ longitudinally granular-strigose grading into a granular to scaly-reticulate area of less intensity, the apical $1/5$ smooth and shining; lateral margin of (2-3) thick-

ened on basal $1/2$; remaining tergites apparently smooth except very weak punctulation visible laterally on tergites 5, 6, and 7 anterior to setal row; epipleurites dully shagreened.

Color: Body color more or less uniformly dull ferrugineous, except sculptured part of tergite (2-3) and basal $1/2$ of tergite 4 are suffused with golden brown while the remaining gastral tergites approach castaneous; legs concolorous with body except testaceous trochanters, fore and mid coxae, and whitish-banded basal $1/6$ to $1/4$ of tibiae; antennae and ovipositor sheaths testaceous, both becoming brown apically; tegulae, maxillary and labial palpi testaceous; wings distinctly banded as in Figure 21; veins brown; basal $1/3$ of stigma pale whitish, remainder brown.

Variation: Paratype females. Agree with holotype in most features, although body color is commonly lighter, dark testaceous, especially in individuals from eastern North America; propodeum, petiole and gaster visibly lighter than remainder of thorax in some individuals, and gaster often of one hue instead of darker apically as in holotype; paratype from New Mexico with the median mesonotal lobe suffused with golden brown; eyes usually a dull greyish, never with any iridescent hue in white light; vertex sculpture sometimes obscured, but sculpture on tergite (2-3) always developed; number of fore tibial spines varies from 25-36 with a row of from 5-9 spines at apex; outer apical lobe of hind tibia with 2-5 spines; variation in measurements and ratios given in Table 2.

Paratype males: In general, variation tends to parallel that in the females.

Paratypes: Canada, Quebec: La Trappe, 2♀♀, 10 July and 2 Aug. 1943 (J. Ouellet) [Montreal, CNC]. U. S. A., Florida: Jackson Co., Fla. Caverns St. Pk., 1♀, 23 June 1961 (H. V. Weems, Jr.) [USNM]. Iowa: Ames, 1♀, 4 Aug. 1951 (W. S. Craig) [USNM]. Maryland: Patuxent Ref., Bowie, 3♀♀, 3♂♂, 9 Aug. 1950 (R. T. Mitchell) [USNM]; Plummers I., 2♂♂, 28 May and 4 July 1911 (J. C. Crawford) [USNM]. New Jersey: Metuchen, Woodwild Park, 5♀♀, 21 Aug. 1953 (377), 10 Aug. 1953 (501), 5 Sept. 1954 (1153), 12 June 1955 (1258) (C. C. Porter) [Porter, MCZ]. New Mexico: Cimarron, 1♀, 23 Aug. 1955, 9500 ft. (D. Townes) [Townes]. New York: Bemus Pt. 1♀, 25 July 1937 (H. K. Townes) [Townes]. North Carolina: Tryon, 1♀, Hopk. U. S. 1577e, Castanea dentata (W. F. Fiske) [USNM]. Virginia: Great Falls, 1♀, 21 July 1962 (G. Steyskal) [USNM]. West Virginia: Hardy Co., Lost River St. Pk., 1♀, 2♂♂, 1-14 Aug. 1960 (K. V. Krombein) [USNM].

Remarks: This species is the largest of the North American Spathius. It may be distinguished by the combination of the long slender straight petiole, very long ovipositor (about 1.6-2.0x FWL), tergite (2-3) sculptured on about basal .75-.80, strongly granular mesopleural disc and mesosternum, and hind tarsomere 3 distinctly longer than tarsomere 5. It is named for Dr. Howard E. Evans in grateful appreciation for his interest and guidance during my Harvard years.

Distribution: Apparently widespread throughout all but the western coast of North America. In addition to the paratype localities I have seen specimens from Colorado, Ohio, Maine, Michigan, Pennsylvania and South Carolina.

Hosts: No hosts are known. The paratype from North Carolina was taken from under the bark of chestnut, Castanea dentata, according to Hopkins No. 1577e.

9. Spathius sequoiae Ashmead

(Figs. 16, 27)

Spathius sequoiae Ashmead, 1889 (1888), Proc. U. S. natn. Mus. 11: 625.

[Type locality: California: Alameda Co. (lectotype female in USNM, Type No. 2925)].

Spathius californicus Ashmead, 1893, Can. Ent. 25: 71. [Type locality:California: Santa Cruz Mts. (holotype male in USNM, Type No. 14660)].
New synonymy.Spathius brunneri Viereck, 1912, Proc. U. S. natn. Mus. 42: 627-628. [Type locality: Montana: Columbia Falls (holotype female in USNM, Type No. 14730)]. New synonymy.

Females: Body length, 2.5-4.1 mm; FWL, 2.1-3.6 mm; ovipositor sheath length, 0.8-2.8 mm. Other measurements and ratios in Table 3.

Head: Flagellomeres 22-32; face transversely strigose-granular and somewhat shining; frons delicately transversely striate to almost smooth and shining; vertex virtually smooth and shining to transversely strigose; temples apparently smooth but usually with faint wrinkled sculpture posteriorly adjacent to occipital carina; ocellar triangle weakly raised, smooth to weakly strigose granular.

Thorax: Lateral areas of prothorax well developed and extending to procoxal cavities, with several irregular oblique cross carinae; remainder of propleura longitudinally strigose to weakly rugose; notauli distinct, crenulate anteriorly, meeting in a broad shallow area of weak rugosity from which often emerge two more or less parallel longitudinal carinae which extend to the posterior margin of mesoscutum; mesonotum abruptly declivous, the lobes evenly granular, the middle lobe sometimes with a faint longitudinal depression medially; scutellar furrow variable, crossed by 3-9 variously developed carinae, some of which are often wrinkled or partially obscure; scutellum slightly projecting, the disc delicately granular to scaly-reticulate and lateral faces irregularly obliquely striate; mesopleural disc highly variable, typically delicately striate, many originating as weak extensions of sternaulus cross carinae and converging posteriorly at speculum, but occasionally almost smooth above sternaulus or weakly scaly-reticulate to delicately strigose-granular; sternaulus relatively broad and well impressed, crossed by several delicate closely spaced cross carinae, the more posterior elements stronger, several curving posteriorly and continuing to mesocoxal cavities, the space following the sternaulus distinctly obliquely striate; prepectal carina complete, prepectal area smooth to irregularly surfaced, with sparse setae; propodeal carinae all sharply defined and distinct; dorsal areas granular to weakly rugose; relative lengths of basal carina and its forks variable; costulae approximately perpendicular to basal forks and directed slightly anteriorly; areola typically an elongate, almost parallel-sided trapezoid enclosing irregular raised sculpture, occasionally broadened to almost diamond-shaped; area petiolaris rectangular to sub-triangular, never longer than $2/3$ of areola and usually devoid of sculpture; fore tibia with 13-33 spines arranged in double to occasionally triple irregular rows and a row of 5-8 spines at apex; outer apical lobe of hind tibia with 2-5 spines; hind coxae weakly obliquely striate dorsally; hind tarsomere 3 about equal to tarsomere 5; subdiscoideus not interstitial; first abscissa of radius shorter than recurrent vein, so that second abscissa of radius and second abscissa of cubitus converge slightly apically.

Abdomen: Petiole granular to irregularly longitudinally strigose apically

and arched at base; tergite (2-3) varying from apparently smooth or very faintly sculptured at extreme base, to a distinct area of weak scaly-reticulate, aciculate or granular sculpture on at most about basal 3/8; remaining tergites smooth, epipleurites nearly always faintly sparsely punctuate; tergite (2-3) weakly thickened laterally at base; ovipositor slightly curved, typically 0.6-0.8x FWL but rarely shorter.

Table 3. Measurements and ratios of selected characters for females of the sequoiae species group. Top line in each instance gives range; number below is for holotype or lectotype.

	<u>sequoiae</u>	<u>canadensis</u>	<u>aphenges</u>
n	27	18	7
number of flagellomeres	22-32 23	21-28 broken	20-25 23
body length (mm)	2.5-4.1 2.7	2.0-3.8 2.9	1.9-3.1 2.8
FWL (mm)	2.1-3.6 2.4	2.0-2.8 2.4	1.8-2.7 2.3
MS/EH	0.41-0.60 0.50	0.40-0.56 0.50	0.49-0.55 0.52
TW/EH	0.58-0.85 0.68	0.61-0.75 0.73	0.60-0.79 0.67
IOD/EH	1.00-1.35 1.18	1.07-1.35 1.14	1.20-1.43 1.24
OTW/OED	0.67-0.92 0.77	0.64-0.83 0.69	0.64-0.82 0.67
OED/OOD	0.71-1.00 0.87	0.75-1.09 0.81	0.81-1.00 0.81
Pet. L/(2-3)L	1.27-1.72 1.71	1.33-1.60 1.56	1.22-1.30 1.22
ICu ₁ /R ₂	0.96-1.27 1.00	0.76-1.22 1.05	0.91-1.00 0.95
OSL/FWL	0.33-0.80 0.63	0.45-0.65 0.54	0.32-0.46 0.43

Color: Body color highly variable from more or less wholly testaceous to piceous, but commonly dark ferrugineous, the head very slightly lighter; typically, the apical 1/3 of the petiole and basal 1/2 of tergite (2-3) are distinctly lighter than the remainder of the gaster and thorax; legs usually lighter than body, especially in darker specimens, hind coxae and legs usually a shade

darker than the fore and mid coxae and legs, the tibiae usually distinctly lighter banded basally; antennae usually testaceous basally, becoming tan to brown apically; maxillary and labial palpi light testaceous; eyes grey, with no trace of iridescence in white light; tegulae testaceous, usually lighter than thorax; fore wings weakly infumated, at most lightly banded (Fig. 27) to subhyaline; veins and stigma tan to brown, the basal $1/3$ of stigma lightened. (The wings have also been figured by Marsh, 1963 and 1965, under S. brunneri.)

Males: Essentially agree with the females in color and sculpture, paralleling the variation noted, though the sculpture, particularly of the frons, vertex and mesopleural disc tends to often be greatly reduced in intensity; however, sculpture on base of tergite (2-3) when present may cover up to the basal $1/2$; also the areola of the male propodeum is often greatly reduced compared to that of the female, and the basal carina thus very long, much longer than its forks; male tarsi (Fig. 16) are proportionately distinctly shorter than those of the female, and hind tarsomere 3 is distinctly shorter than tarsomere 5; size ranges from 1.5-3.7 mm; Marsh (1965) has figured the genitalia.

Remarks: Spathius sequoiae was described by Ashmead (1889) from two females, one of which bears the label "Spathius sequoiae Ashm." in Ashmead's handwriting. I have designated this specimen as lectotype and the other becomes a paralectotype; both bear three additional labels "Alameda Co. Cal.", "Parasite on Col. larva on redwood", and the red "USNM Type No. 2925".

In addition to the types of each of the original three species, I have seen several short series of reared specimens from various species of coniferous trees in western North America, and measured about 40 selected individuals of both sexes. I have been unable to find any consistent differences by which specimens may be separated, and it appears that the chief way in which they were distinguished in the past was by sorting according to host. Spathius californicus, based on a single male, has always been an uncertain species, and was never formally described beyond the characters given by Ashmead (1893) in his "Table of Species". It was distinguished from S. sequoiae in opposite parts of his table on whether the wings appeared hyaline (californicus) or banded (sequoiae), an inadequate character. Both are from adjacent localities in California (Santa Cruz Mts. and Alameda Co.) and of opposite sex, a situation immediately suspect. Viereck (1912) described Spathius brunneri from two females reared from Pissodes in Pseudotsuga from Columbia Falls, Montana (Hopkins No. 8574). He failed to note its similarity to sequoiae, instead thinking it closest to S. unifasciatus Ashmead (=trifasciatus Riley), comparing the two in his description. Actually, they are quite different, having only superficial similarity in size and body coloration, particularly in the lightened area at the apex of the petiole and base of tergite (2-3). The very stout petiole of the type is atypical, that of the paratype being the more usual case.

Diagnosis: A highly variable species, S. sequoiae may be characterized by the weakly infumated fore wings (Fig. 28), well developed lateral areas of the prothorax, delicately transversely striate vertex, weak to almost obscure sculpture on about basal $3/8$ of tergite (2-3), and the form of the sternaulus and mesopleural disc. It is most closely related to S. canadensis, from which it may usually be distinguished by the longer ovipositor (0.60-0.80x FWL versus 0.45-0.65x FWL in canadensis) and presence of more spines on the fore tibia (15-33 in irregular double and sometimes triple rows versus 11-23 in irregular single to double rows in canadensis). Qualitatively, canadensis, typically a smaller and more slender species, tends to have a more scaly reticulate mesopleural disc than sequoiae, and also may show additional weak sculpture follow-

ing the basal 3/8 sculpture on tergite (2-3). Males of the two differ additionally in relative lengths of tarsi to tibiae, *sequoiae* males having relatively shorter tarsi (Fig. 16) (hind tarsus/tibia ratio of 0.66-0.88, versus 0.84-0.96 in *canadensis* males) but small specimens may be virtually inseparable.

Indeed, until additional reared series and biological information are available, I regard this separation as tentative, but prefer to retain the two as full species rather than subsets of a polytypic species. Both *sequoiae* and *canadensis* are parasites of scolytids occurring in coniferous trees, *canadensis* being commonly reared from spruce in eastern North America and *sequoiae* from a wide variety of coniferous trees (including spruce) in western North America. A series from *Picea glauca* from Seebe, Alberta (CNC) possess some apparently intermediate characters. Another from redwood in Mill Valley, California (CAS) includes two females with very short ovipositors which would key to *aphenges* but may be distinguished by the greater petiole to tergite (2-3) ratio (1.27-1.72 versus 1.22-1.30 in *aphenges*) and the absence of sculpture beyond the basal 3/8 of tergite (2-3).

Distribution: Widespread throughout western North America, north to Alaska. I have seen material from Alaska, California, Colorado, Idaho, Montana, Oregon, New Mexico, Utah, Washington, British Columbia and Alberta.

Hosts: No hosts were previously recorded for *Spathius californicus*. *Spathius sequoiae* is recorded as a parasite of *Phloeosinus sequoiae* Hopkins and *P. punctatus* LeConte, both scolytids (Muesebeck et al., 1951, DeLeon, 1952, and Bushing, 1965). I have confirmed these records and the specimens on which they are based bear Hopkins Nos. 15815a and 18161-b. *Spathius brunneri* is recorded from *Pissodes* sp. (Curculionidae) and the scolytids *Pseudohylesinus nebulosus* (LeConte) and *Scolytus ventralis* LeConte (Viereck, 1912, Bedard, 1938, Muesebeck et al., 1951, Bushing and Bright, 1965, Bushing, 1965, Muesebeck, 1967, and Asraf and Berryman, 1969). I have also confirmed these records.

According to the material before me, *S. sequoiae* has been reared from scolytids in the following trees: *Pseudotsuga*, *Tsuga*, *Chamaecyparis*, *Larix*, *Sequoia*, *Thuja*, *Abies* and *Picea*. The majority of the records are from *Pseudotsuga*; associated insects are listed under Hopkins Nos. 8574, 10764b, 20225, 31532-F, 31713-D, 35312-E, 353560 and 39696b. Additional hosts not recorded above include the scolytids *Dendroctonus pseudotsugae* Hopkins and *Scolytus tsugae* Swaine. Host records from *Tsuga* include *Scolytus* sp., recorded under Hopkins Nos. 1849n2, 2174e5, 2174g2a and 19858. The single record from *Chamaecyparis* (Hopkins No. 33316c) lists *Phloeosinus sequoiae* and *P. punctatus* as associated insects. The records from *Sequoia* and *Thuja* are listed above as the hosts of *Spathius sequoiae*. Hopkins No. 34214B-7 records *Dendroctonus obesus* as the host in *Picea engelmanni*. According to D. F. J. Hilton (pers. comm.) the series he reared from *Picea glauca* in Alberta was associated with the following scolytids: *Carphoborus intermedius*, *Dryocoetes affaber*, *Pityophthorus murrayanae*, *Polygraphus rufipennis*, *Scolytus piceae* and *Trypodendron lineatum*. No hosts are recorded from *Larix*.

10. *Spathius canadensis* Ashmead

Spathius canadensis Ashmead, 1891, Can. Ent. 23:2. [Type locality: Canada: Ottawa (holotype female in USNM, Type No. 52649)].

Spathius claripennis Ashmead, 1893, Can. Ent. 25: 70, 72. [Type locality:

West Virginia: Morgantown (lectotype male in USNM, Type No. 2148)].
New synonymy.

Spathius clavipennis [sic] Ashmead, in Hopkins, 1892, Insect Life 4: 257.
Spathius tomici Ashmead, 1893, Can. Ent. 25: 71. [Type locality: West Virginia: Morgantown (holotype female in USNM, Type No. 52648)].
New synonymy.

Females: Body length, 2.0-3.8 mm; FWL, 2.0-2.8 mm; ovipositor sheath length, 0.95-1.7 mm. Other measurements and ratios in Table 3.

Head: Flagellomeres 21-28; face transversely strigose-granular; frons varying from almost perfectly smooth to finely transversely striate; vertex smooth and shining to delicately transversely strigose; temples typically with faint irregular sculpture posteriorly adjacent to occipital carina; ocellar triangle slightly raised, smooth to faintly strigose-granular.

Thorax: Lateral areas of prothorax moderately well developed extending to precoxal cavities and with several irregular oblique cross carinae; notauli distinct, shallowly crenulate anteriorly, meeting in a slightly depressed weakly rugose area from which two weak carinae usually extend to the posterior margin of the mesoscutum; mesonotum abruptly declivous, the lobes evenly scaly-reticulate to granular; scutellar furrow variable, with as many as 8 cross carinae but often with a single well developed medial carina flanked by weaker ones; scutellar disc scaly-reticulate to weakly granular; mesopleural disc variable, either nearly smooth above sternaulus or weakly scaly-reticulate to delicately strigose granular; sternaulus highly variable, from strongly impressed and crossed by several fine closely spaced carinae, the more posterior elements apparently continuing and curving posteriorly to mesocoxal cavities, to almost obscured, scaly-reticulate, the cross carinae indistinct or irregular and none distinctly curving posteriorly to mesocoxal cavities; prepectal carina usually complete but often weak or nearly obscured immediately above sternaulus; prepectal area more or less smooth with sparse setae and sometimes with weak irregular surface rugosity; propodeal carinae typically distinct and well defined; dorsal areas granular to weakly rugose; areola usually trapezoidal, slightly longer than broad (sometimes very elongate), enclosing weak irregular sculpture; basal carina usually not longer than its forks; fore tibia with 11-24 spines arranged in irregular single to double rows and a row of 5-7 spines at apex; outer apical lobe of hind tibia with a row of 3-5 spines; hind coxae weakly obliquely striate dorsally; tibiae and tarsi usually very slender; subdiscoideus not interstitial.

Abdomen: Petiole irregularly longitudinally strigose-granular and arched at base; epipleurite of petiole variable, sometimes more than half of the petiole length; tergite (2-3) usually with distinct area of granular to scaly-reticulate sculpture on about basal $3/8$ to $4/9$, with or without an additional very weak scaly-reticulate area following a narrow unsculptured line; remaining tergites typically smooth, but sometimes with sparse punctulation anterior to the transverse row of setae; epipleurites usually very faintly punctulate; lateral margin of tergite (2-3) usually thickened weakly at base; ovipositor slightly curved, usually 0.45-0.62x FWL.

Color: Body color usually uniformly dark shining testaceous, the gaster beyond the basal half of tergite (2-3) usually distinctly darker; legs concolorous with body or slightly lighter, hind coxae and legs sometimes a shade darker than fore and middle coxae and legs, the tibiae indistinctly lighter banded at bases; eyes grey to faintly iridescent green in white light; antennae testaceous, often lighter than head at base, becoming light brown apically; ovipositor sheaths usually brown, sometimes contrasting strongly with the lighter gaster; fore wing infumation variable, usually weakly infumated to sub-hyaline, but one

series from Wood Co., Wisconsin (RDS) has several individuals with well defined fasciations; veins and stigma tan or stramineous, the basal 1/3 of stigma usually lighter.

Males: Essentially agree with the females in color and sculpture, paralleling the variation noted; size smaller, 1.6-2.5 mm, and number of flagellomeres varies from 19 to 25; body color often much darker than for females, to nearly piceous, except lighter base of gaster and legs; wings usually hyaline to sub-hyaline; sculpture on base of tergite (2-3), when present, may cover as much as 1/2 of tergite; tarsi not especially shortened, hind tarsus to tibia ratio of 0.84-0.95.

Remarks: Since 1936, *Spathius canadensis* Ashmead has become firmly entrenched in the literature and almost automatically applied to any *Spathius* reared from elm. However, this association is incorrect (see "Remarks" for *S. benefactor*). Detailed study of Ashmead's type reveals it to agree most closely with that of *S. tomici* and with females associated with the type male of *S. claripennis*. Ashmead's concept of *canadensis*, based upon a single female from an unknown host, was insufficiently stringent, for specimens bearing his *canadensis* determination labels belong to at least three different species. It is easy to appreciate how confusion could arise, for the type belongs to a difficult complex of species and bears superficial resemblance to several other species. These misplaced *canadensis* specimens were probably identified on the basis of their overall "gestalt": chiefly their relatively small size, short ovipositor and sculpture of tergite (2-3).

The female of *S. claripennis** was previously unknown; I base my associations on three short series of both sexes from spruce: one from Webster, New Hampshire (Hopkins No. 3726c), another from Cherry Mt., New Hampshire (Hopkins No. 17614c) and the third from Rensselaerville, New York (MCZ). The males from these series closely match Ashmead's type of *claripennis*, which is an unusually small individual, and the females essentially agree with the type of *S. tomici*, described in the same paper. The type of *tomici* appears superficially different due to the strongly arched petiole with its epipleurite extending over half of the petiole length, but these characters are highly variable. The type of *S. canadensis* falls readily within the range of variation exhibited by *claripennis* and *tomici*. At first glance it might appear different due to the presence of weak punctulation which it exhibits anterior to the setal rows on tergites 4-7. However, by itself punctulation is an unreliable character, for commonly it is variously expressed within series from several *Spathius* species. Furthermore, even when present it may not be readily apparent unless the gastral tergites are somewhat distended to expose the area anterior to the transverse row of setae on each.

Diagnosis: *Spathius canadensis* may be distinguished from its closest relative, *S. sequoiae*, by its generally smaller, more slender body and smaller

* *Spathius claripennis* was apparently based on two males, according to numbers on Hopkins' original manuscript for his 1892 paper. The specimen bearing the number 2463, according to Hopkins' paper, emerged on April 20, 1892, agreeing with Ashmead's statement in his description. A second individual with the same rearing information but bearing number 2463a is also listed in the original manuscript with no date of emergence given and with the name *Spathius claripennis* written in the margin. Accordingly, I designate as lectotype the specimen bearing number 2463 and the other specimen (2463a) is thus a paralectotype.

OSL/FWL ratio (0.45-0.65 versus 0.60-0.80 in sequoiae). Additional characters are given in the key; see also "Diagnosis" for S. sequoiae.

Distribution: Probably widespread throughout northern North America, south to the higher elevations of North Carolina. I have seen specimens from the following states and provinces: Alberta, British Columbia, Maine, Manitoba, Michigan, New Hampshire, New York, North Carolina, Ontario, South Dakota, Washington, West Virginia and Wisconsin.

Hosts: Spathius canadensis, as defined here, is apparently parasitic upon Scolytidae attacking the smaller branches and crown of spruce, fir, larch and pine. The following are regarded as valid host records: Polygraphus rufipennis, Dryocoetes autographus, Ips pini, Pityophthorus balsameus, Orthotomicus caelatus, Scolytus piceae and Cryphalus sp.

Unfortunately, due to the confusion surrounding the identity of S. canadensis in the past, there have been falsely recorded, under this name, at least 19 hosts representing four coleopterous families from a diverse range of trees. (For a fairly complete summary, see Bushing, 1965.) In the following paragraphs, the interested reader will find a discussion of these.

The first hosts for S. canadensis were reported by Hopkins (1892) and included three bark beetles, Phloeosinus graniger (= dentatus), Tomicus sp. and Dryocoetes americanus (= autographus), and the weevil Magdalis olya, from red cedar, white pine, fir and hickory, respectively; the canadensis specimens correlated with these bear, according to Hopkins' original manuscript, the numbers 2932 (and 2674, 3066), 2589, 2442 and 5180, respectively. Of these, I have been able to locate only 2442, which is S. brachyurus; although unconfirmed, those from Phloeosinus would almost certainly be S. impus.

The following year, Hopkins (1893b) added the buprestid Agrilus otiosus from hickory to the list, and furnished specific identification for the Tomicus (= Ips grandicollis), but made no mention of either Dryocoetes or Magdalis. Unable to associate names with specimens, I suggest they be doubted, especially Agrilus which was probably a host of S. simillimus.

In 1899, Hopkins added the weevil Copturus (= Cylindrocopturus) longulus from pine, another record that I am unable to confirm.

Scolytus rugulosus in apple was recorded as a host of canadensis by Schedl (1932) based on a determination by A. D. Cushman. I suspect that these specimens will probably be found to be S. benefactor.

MacAloney (1930) records Pissodes strobi (Curculionidae) which seems possible, but is again unconfirmed.

In 1936, Kaston and Becker added three new hosts from elm: Hylurgopinus rufipes, Magdalis barbata and M. armicollis. I have seen their specimens and many subsequent series reared from elm, and all should be henceforth recorded as hosts for the new species, Spathius benefactor. Pechuman (1937) added Scolytus multistriatus and Saperda tridentata from elm, and Hoffman (1938) recorded Leperisinus aculeatus from ash; these should also be changed to hosts of S. benefactor.

Hetrick (1940) listed Dendroctonus frontalis from pine; this should be transferred to Spathius pallidus. Beal and Massey (1945) report canadensis from Scolytus quadrispinosus in hickory, probably erroneous, although I have been unable to locate their specimens.

In summary, of all the hosts previously listed for Spathius canadensis, none can be confirmed for this species as it is presently defined.

The only host record previously recorded for Spathius claripennis was Ashmead's original record from the scolytid Polygraphus rufipennis under bark of Abies nigra; subsequent references to this host are listed by Bushing

(1965) under the name P. poligraphus L.

The following scolytid hosts are recorded for Spathius tomici: Dryocoetes autographus from spruce (Hopkins, 1893a); Pityophthorus balsameus from balsam fir (Felt, 1906); Orthotomicus caelatus and Scolytus piceae from larch (Blackman and Stage, 1918); Phloeosinus canadensis and P. dentatus from cedar (Schedl, 1932, and Beal and Massey, 1945). Subsequent references to each are listed by Bushing (1965). Of these, I have seen only specimens of Schedl and Beal and Massey; both records should be transferred to Spathius impus. The others, except possibly Dendroctonus simplex, seem reasonable insofar as the species is currently defined.

Previously unrecorded hosts include the scolytids Cryphalus sp. (Hopkins No. 2871) and Ips pini (Say). I have reared S. canadensis in New York from white spruce in association with Polygraphus rufipennis (Kirby), Dryocoetes autographus (Ratz.) and Crypturgus atomus LeConte (det. D. E. Bright), all Scolytidae.

11. Spathius aphenges, new species

(Fig. 26)

Holotype. - female, California: El Dorado Co., xi-1963 [no collector label], ex. Pinus lambertiana with Orthotomicus latidens [USNM Type No. 70502].

Description of type female: Body length, 2.5 mm; FWL, 2.3 mm; ovipositor sheath length, 1.0 mm. Other measurements and ratios in Table 3.

Head: Flagellomeres 23; face shining almost smooth except for weak transverse rugosity; frons nearly smooth and shining with very faint transverse striation; vertex smooth and polished; temples smooth; ocellar triangle weakly raised, smooth.

Thorax: Lateral areas of prothorax well defined, relatively broad and crossed by several oblique carinae; remainder of propleura finely horizontally strigose to smooth; notauli shallowly crenulate anteriorly, meeting in a small slightly depressed area of weak rugosity; mesonotum moderately declivous, the lobes evenly granular; scutellar furrow lacking sharp well defined cross carinae, but with 3-5 irregular variously developed carinae; scutellum slightly raised, the disc evenly granular; mesopleural disc smooth and shining, becoming abruptly rugose on dorsal anterior part above prepectal area; sternaulus deeply impressed with about 7 poorly defined cross carinae, the posterior margin clearly delimited and followed by a smooth space to mesocoxal cavities; mesosternum smooth; prepectal carina complete; prepectal area covered by sparse setae, otherwise apparently smooth with faint basal irregularities; propodeal carinae sharp and well defined; dorsal areas granular to weakly rugose; basal carina about as long as its forks; costulae inserted at about right angles to basal forks; areola approximately diamond-shaped, about 1.6x as long as basal carina and enclosing weak rugosity; fore tibia with 14 spines arranged in a single row with a row of 6 spines at apex; outer apical lobe of hind tibia with a row of 5 spines; hind coxae with weak oblique striae dorsally; subdiscoideous not interstitial.

Abdomen: Petiole arched basally, dorsally coarsely granular to rugose, becoming longitudinally strigose apically; tergite (2-3) prominently granular on basal 4/9, followed by a narrow smooth area and then 2/9 scaly-reticulate area of much less intensity, the apical 1/3 smooth; lateral margin of tergite

(2-3) weakly thickened at base; ovipositor much shorter than abdomen, about 0.43x FWL.

Color: Head shining light brown weakly suffused with dirty yellow in malar area and lower clypeus; prothorax dirty testaceous; remainder of thorax and propodeum light brown, the propodeum slightly lighter; petiole and tergite (2-3) dirty testaceous, remainder of gaster slightly darker, almost a brown; ovipositor sheaths testaceous at base, becoming brown apically; antennae testaceous basally, decidedly lighter than head, becoming light tan apically; maxillary and labial palpi, tegulae, coxae and legs wholly light testaceous, distinctly lighter than body; eyes gray, not at all iridescent in white light; wings weakly infumated as in Figure 26; veins testaceous to tan, stigma light brown, the basal 1/3 lighter stramineous.

Variation: Paratype females. Body color varies from about wholly testaceous to nearly ferruginous; appendages (except ovipositor sheaths) of lighter individuals may not particularly contrast with body as in the type; eyes never iridescent; number of fore tibial spines varies from 11-17; sculpture of frons may be totally obscured in some individuals and it is never stronger than in type; vertex and temples nearly always smooth, though occasionally faint irregularity occurs; sculpture on basal part of tergite (2-3) always present, though sometimes reduced in intensity, but sculpture on middle part of tergite is often obscured or only faintly scaly-reticulate; sternaulus development somewhat variable, sometimes barely developed with no obvious cross carinae, the whole of the mesopleuron (except dorsal part) appearing smooth; fore wings of some individuals subhyaline; variation in measurements and ratios given in Table 3.

Paratype males: The two paratype males agree essentially with the females.

Paratypes: 1♀, 1♂, same data as holotype. [USNM]. U. S. A., California: Strawberry, 1♀, 22 July 1962, Flight trap, Hopkins No. 37714GGG (W. D. Bedard) [USNM]. Oregon: Ashland, 4♀♀, 1♂, 4 June 1914, reared Pinus lambertiana, Hopkins No. 10884d (P. D. Sargent) [USNM].

Remarks: The small size and very short ovipositor (less than 0.5x FWL) immediately distinguish this species and Spathius parvulus from all the other Nearctic species. The combination of the smooth, shining vertex, non-iridescent eyes and only weakly infumated fore wings (compare Figs. 26 and 30) will usually readily distinguish aphenges from parvulus. In addition, aphenges has a relatively shorter petiole (ratio of petiole length to tergite (2-3) length, 1.22-1.30 in aphenges versus 1.33-1.45 in parvulus) and a broader temple (TW/EH, 0.60-0.79 in aphenges versus 0.50-0.63 in parvulus). Occasional individuals of S. sequoiae having ovipositors less than 0.5x FWL may be distinguished by the characters discussed in the "Diagnosis" section under that species.

Distribution: Probably widespread in western North America. In addition to the paratype localities, I have seen specimens from Idaho, Washington, Alberta and British Columbia.

Hosts: The type series was reared from the scolytid Ips latidens LeConte in sugar pine, Pinus lambertiana. The paratype series from Oregon was also reared from P. lambertiana, according to Hopkins No. 10884d, and were "ex. 2 cones of 1913 crop killed by cone beetle." Godwin and Odell's (1965) reference to Spathius sp. emerging from cones infested with this beetle (Conophthorus coniperda (Schwarz)) no doubt refer to this species, although I have not seen their specimens. A specimen from Alberta is labeled as being from the scolytid Phthorophloeus puberulus (LeConte), which according to Chamberlin (1939) attacks the tops and limbs of Douglas fir, Pseudotsuga taxifolia. I have

also seen a series of *Spathius aphenges* reared from *Scolytus abietis* Blackman in grand fir, *Abies grandis*, from Idaho. In addition, single females were reared from *Pinus contorta* in British Columbia and *P. ponderosa* in Oregon (Hopkins No. 10074), the latter in association with several borers and the scolytid *Pityophthorus* sp.

12. *Spathius pallidus* Ashmead

(Fig. 28)

Spathius pallidus Ashmead, 1893, Can. Ent. 25: 72, 74. [Type locality: West Virginia: Morgantown. (holotype female in USNM, Type No. 2152)].

Spathius pollidus [sic] Ashmead, in Hopkins 1893a and 1893b, Bull. W. Va. agric. Exp. Stn. 31: 145 and 32: 346.

Females: Body length, 2.2-3.8 mm; FWL, 1.9-3.2 mm; ovipositor sheath length, 1.2-2.1 mm. Other measurements and ratios in Table 4.

Head: Flagellomeres 26-33; face coarsely transversely strigose-granular, ending abruptly at malar space; eyes very slightly emarginate adjacent to antennal insertions; frons transversely striate; vertex uniformly transversely strigose, becoming less strong or scaly-reticulate to nearly smooth at eyes; temples smooth along eyes, becoming moderately strigose posteriorly, more or less parallel to occipital carina; malar space rarely greater than $1/2$ EH; ocellar triangle broad, weakly raised and delicately granular to smooth.

Thorax: Lateral areas of prothorax moderately developed, losing distinctness posteriorly in the irregular strigose-granular sculpture of remainder of prothorax; notauli distinctly impressed and crenulate anteriorly, merging to a broad, slightly depressed usually moderately rugose area; mesonotum moderately declivous, robust, greatest width at least equal to greatest length, usually slightly broader than long, the lobes evenly granular; scutellar furrow crossed by 3-10 more or less evenly spaced straight carinae; scutellum broad, weakly projecting, the disc evenly granular right to the truncate posterior margin, there never being any rugosity posteriorly; mesopleural disc rarely partly smooth, but typically strigose-granular above sternaulus, this becoming much more pronounced dorsally below wings; sternaulus broad, usually well impressed, crossed by several closely spaced variously developed carinae, many of which may appear to extend onto mesopleural disc; the space posterior to the sternaulus usually with 2-6 curved striae extending from the posterior end of the sternaulus to the mesocoxal cavity; prepectal carina weak immediately above the sternaulus; prepectal area nearly smooth, with weak surface irregularity; propodeal carinae all more or less distinct, often with numerous short side branches; dorsal areas granular to weakly rugose; basal carina usually shorter than its forks; the segments of the basal forks anterior to the costulae insertions about 2-3x the posterior segments, the areola thus an elongate trapezoid enclosing an area of irregular weak reticulation; area petiolaris rectangular, about $1/3$ as long as areola and lacking distinct sculpture centrally; fore tibia with 18-25 spines arranged in an irregular double row with a row of 5-8 spines at apex; outer apical lobe of hind tibia with a row of 3-5 spines situated somewhat anteriorly; claws often with prominent pulvilli; subdiscoideus not interstitial; first intercubitus typically slightly longer than second abscissa of radius.

Abdomen: Petiole arched at base, dorsally coarsely granular to longitu-

dinally strigose; tergite (2-3) with a distinct area of granular sculpture on about basal 2/5 to 5/11, followed almost immediately by another area of less well developed granular or scaly-reticulate sculpture extending nearly to transverse row of setae, the apical margin beyond the setal row smooth; remaining tergites vary, frequently apparently smooth, but often with weak transverse bands of faint scaly-reticulation or sparse punctulation anterior to the setal rows on at least the 4th tergite; ovipositor from 0.60-0.72x FWL.

Color: Body color typically wholly tawny yellow to light brown, but varying from light honey yellow to light ferrugineous, the gaster beyond the basal 2/3 of tergite (2-3) sometimes slightly darker; coxae and trochanters concolorous, usually a shade lighter than the body, from stramineous to light testaceous; femora and tibiae concolorous with body, the basal 1/3 to 1/4 of tibiae lighter banded; tarsi testaceous, the ultimate tarsomere and claws usually slightly darker than others, typically dull ferrugineous; antennae testaceous to light brown, darkening gradually toward apex; ovipositor sheaths testaceous at base, becoming dark brown on about apical 1/3; eyes light gray, sometimes with a weak iridescent hue in white light; fore wing darkly infumated and distinctly banded (Fig. 28); veins light to dark brown; stigma brown, the basal 1/3 lighter, dirty yellow to stramineous.

Males: Agree with females in most respects and parallel the variation noted, except that tergite (2-3) has a larger area of well developed granular sculpture covering about basal 1/2 followed by another area of less strong sculpture as in female, and the areola is often reduced in size, sometimes to the form of a small diamond, the basal carina thus longer than its forks; also, small individuals sometimes have marked reduction in sculpture, particularly that of vertex which may appear nearly smooth.

Remarks: The holotype, USNM Type No. 2152, bears the printed label "3768 Hopk. W. Va." which is not in Hopkins' original manuscript for his 1892 paper. Nor could I find it in the Hopkins card file. It also bears Ashmead's handwritten label "Spathius pallidus Ashm." The type catalog says two specimens were included, but I have only located the one, and consider it the holotype. It is lacking the antennae and both fore wings.

Diagnosis: Spathius pallidus is best distinguished by the combination of the typically wholly tawny yellow body with the gaster at most slightly darker beyond the base of tergite (2-3), the robust mesonotum and strigose sculpture on the mesopleural disc. It most resembles S. impus and S. parvulus, sharing the narrow temples and narrow striated vertex. It may be distinguished from impus by its greater OTW/OED ratio (0.80-0.93 versus 0.60-0.83 in impus) and the presence of additional sculpture on the middle portion of tergite (2-3) which is absent in impus. S. parvulus differs in having a shorter ovipositor (typically less than half of FWL compared to 0.60-0.70 in pallidus) and a smooth mesopleural disc; also the form of the vertex sculpture differs (see Fig. 25).

Distribution: Southeastern United States north to Massachusetts. I have seen material from the District of Columbia, Georgia, Louisiana, Maryland, Massachusetts, Mississippi, North Carolina, South Carolina, Texas and Virginia.

Hosts: Four hosts are recorded, the scolytids Ips grandicollis (Eichhoff) (= Tomicus cacographus LeConte) and Dendroctonus frontalis Zimmermann, the buprestid Chrysobothris femorata (Oliv.) and the cerambycid Callidium variabilis L. A resumé of the literature references to these hosts is given in Bushing (1965). Based on the material I have seen, the latter two hosts are probably incorrect, being most likely based on misidentifications of Spathius

simillimus or S. floridanus.

Much of the material I have seen is reared under various Hopkins numbers, all from various species of *Pinus*. The most frequently cited host is D. frontalis (Hopkins Nos. 10099v, 46768, 46847, and 17843d1b). New host records include the scolytid Ips avulsus (Eichhoff) (Hopkins No. 3350j) and the weevils, Pissodes nemorensis Germ. (Hopkins No. 6885h) and P. approximatus Hopkins (Hopkins No. 3810d). Hettricks' (1940) reference to Spathius canadensis as parasitic on Dendroctonus frontalis (and subsequent references to this record in Bushing, 1965) should be changed to this species, as I have seen his specimens.

13. Spathius parvulus, new species

(Figs. 25, 30)

Holotype. - female, New Mexico: Vermego, Bred Sept. 11, '08, Pinus ponderosa, Hopk. U. S. 2410a (A. D. Hopkins) [USNM Type No. 70503].

Description of type female: Body length, 2.0 mm; FWL, 1.9 mm; ovipositor sheath length, 0.75 mm. Other measurements and ratios in Table 4.

Head: Flagellomeres 21; face delicately strigose-granular; frons delicately transversely striate; vertex delicately strigose, the striae curving medially and anteriorly toward ocellar triangle (Fig. 25); temples apparently smooth with extremely faint irregularity posteriorly near occiput; ocellar triangle weakly raised with delicate granular sculpture which continues weakly onto vertex.

Thorax: Lateral areas of prothorax shallow, but distinct with several oblique cross carinae on smooth background; remainder of propleura finely granular; notauli shallowly crenulate anteriorly, losing definition posteriorly except for faint irregular rugosity in area of convergence; mesonotum robust, strongly declivous, the lobes evenly granular; scutellar furrow with 4 evenly spaced carinae; scutellum weakly convex, the disc uniformly granular; mesopleural disc apparently smooth or faintly scaly-reticulate, with delicate, predominantly horizontal striae dorsally; sternaulus a broad, shallow depression with obscure traces of a few cross carinae; prepectal carina complete; prepectal area smooth, sparsely hairy with some irregular rugosity ventrally; propodeal carinae all distinct and well developed; dorsal areas wholly granular; basal carina slightly shorter than its forks; costulae approximately perpendicular to basal forks; areola and area petiolaris distinctly separated, the areola about 1.6x as long as area petiolaris and granular; area petiolaris rectangular with one carina across basal third; fore tibia with 18 spines arranged in an irregular single row with a row of 6 spines at apex; outer apical lobe of hind tibia with 3 spines; tarsomere 5 distinctly longer than tarsomere 3 on all legs; subdiscoideus not interstitial; recurrent vein distinctly longer than first abscissa of radius.

Abdomen: Petiole about as long as middle tibia and strongly arched at base; petiole sculpture granular dorsally at base becoming irregularly longitudinally strigose at apex; tergite (2-3) with prominent granular to scaly-reticulate sculpture on about basal 2/3, the remaining 1/3 smooth; sculptured portion of two distinct intensities, basal 3/5 much stronger, abruptly becoming much less intense for remainder; lateral margin of tergite (2-3) weakly thickened at base; remaining tergites smooth; ovipositor much shorter than abdomen.

Color: Body color wholly testaceous except for gaster beyond basal 2/3 of tergite (2-3) which is dull ferrugineous; ovipositor sheaths brown; legs unicolorous, testaceous, the tibiae not distinctly banded at base, the claws and

ultimate tarsomeres slightly darker; antennae testaceous, gradually becoming light brown apically; palpi testaceous; eyes with a distinct bluish-green iridescent hue in white light; wings lightly infumated as in Figure 30.

Variation: Paratype females. The three paratype females show no significant variation, although the intensity of the vertex striation shows some tendency for reduction (but still discernable); number of fore tibial spines varies from 16-18. Variation in measurements and ratios given in Table 4.

Paratype males: Similar to females in all respects except that sculpture on tergite (2-3) is much stronger and of approximately uniform intensity throughout, covering about basal $3/4$ of the tergite; however, vertex striation tends to be considerably reduced in intensity to almost smooth; lateral margin of most tergites thickened; junction of costella and radiella of hind wing slightly thickened.

Paratypes: 3♀♀, 3♂♂, same data as holotype.

Remarks: This species is apparently related to Spathius impus and shares with it the relatively narrow vertex and temples. It differs from it chiefly by the shorter ovipositor (typically less than 0.5x FWL versus 0.5-1.02x FWL in impus) the more extensively sculptured tergite (2-3), and the form of the vertex sculpture (Fig. 25), which also distinguishes it from the other Nearctic species. About two dozen specimens from several localities in eastern United States are tentatively included here, but may later prove to be a distinct species. These are similar to the type series, but have the face more coarsely granular, the vertex simply transversely strigose, and are generally darker colored.

Distribution: The type series is from Vermego, New Mexico. I was unable to find this locality in Hammond's New World Atlas and think it is likely a misspelling of Vermejo, north of Maxwell in Colfax County. I have also seen specimens from South Dakota and Colorado. Specimens from eastern North America tentatively placed here are from Maine, Maryland, Massachusetts, New Hampshire, New York and West Virginia.

Hosts: The type series was recorded under Hopkins No. 2410a which lists Tomicus [= Ips] sp. in ponderosa pine as the apparent host. Three specimens from Winchester, Massachusetts (N. E. For. Ins. Lab No. 12472y2) are labeled "ex. Pissodes strobi" (white pine weevil).

14. Spathius impus, new species

(Fig. 18)

Holotype.- female, Connecticut: East River, reared 31 May 1916, Hopkins No. 10762a, Juniperus virginiana (C. R. Ely) [USNM Type No. 70504].

Description of type female: Body length, 2.9 mm; FWL, 2.5 mm; ovipositor sheath length, 1.7 mm. Other measurements and ratios in Table 4.

Head: Flagellomeres 24; face transversely strigose-granular; frons weakly transversely striate; vertex transversely strigose; temples smooth adjacent to eyes, becoming weakly wrinkled strigose posteriorly; ocellar triangle weakly granular, very slightly raised.

Thorax: Lateral areas of prothorax weakly developed, shallow, smooth with a few indistinct delicate oblique cross carinae, becoming obliterated in the finely granular-strigose sculpture of remainder of prothorax; notauli distinct, shallowly crenulate anteriorly, meeting in a slightly depressed area with weak surface irregularity dominated by two elongate subparallel longitudinal carinae

which extend to the posterior margin of mesonotum; mesonotum rather abruptly declivous, the lobes evenly granular; scutellar furrow narrowest at mid-point, with apparently 5 cross carinae; scutellar disc uniformly delicately granular or scaly-reticulate; mesopleural disc delicately granular or scaly-reticulate above sternaulus, becoming irregularly longitudinally strigose dorsally beneath wings; sternaulus broad, well impressed, with 8 or 9 weak but distinct cross carinae; prepectal carina complete; prepectal area more or less smooth with weak surface irregularity; propodeal carinae all developed, but rather delicate; dorsal areas granular to weakly rugose-reticulate; basal carina a little more than half as long as its forks; costulae more or less perpendicular to forks; areola elongate, a little more than twice as long as broad, the sides

Table 4. Measurements and ratios of selected characters for females of the pallidus species group. Top line in each instance gives range; number below is for holotype or lectotype.

	<u>pallidus</u>	<u>parvulus</u>	<u>impus</u>	<u>comes</u>
n	10	13	17	10
number of flagellomeres	26-33 broken	21-29 21	20-28 24	26-37 36
body length (mm)	2.2-2.8 3.4	2.0-3.3 2.1	1.7-3.3 2.9	2.5-5.1 5.0
FWL (mm)	1.9-3.2 broken	1.8-2.8 1.9	1.5-2.9 2.5	2.3-3.9 3.9
MS/EH	0.44-0.50 0.50	0.34-0.58 0.35	0.43-0.58 0.48	0.47-0.59 0.54
TW/EH	0.54-0.71 0.69	0.50-0.63 0.55	0.50-0.63 0.56	0.63-0.78 0.69
IOD/EH	1.03-1.21 1.15	0.96-1.26 1.05	1.00-1.19 1.12	1.09-1.28 1.14
OTW/OED	0.80-0.93 0.92	0.71-0.91 0.80	0.60-0.83 0.69	0.68-0.88 0.88
OED/OOD	0.70-0.81 0.73	0.80-1.00 0.91	0.85-1.11 0.93	0.64-0.82 0.64
Pet. L/(2-3)L	1.40-1.70 1.60	1.33-1.45 1.38	1.26-1.65 1.59	1.04-1.59 1.30
ICu ₁ /R ₂	0.93-1.17 -	0.87-1.14 1.11	0.92-1.20 1.08	0.87-1.07 0.94
OSL/FWL	0.60-0.72 -	0.35-0.64 0.39	0.50-1.02 0.68	0.91-1.57 1.26

sub-parallel, enclosing an area with several weak irregular transverse carinae; fore tibia with about 15 spines arranged in irregular rows of 2, and a row of 5 or 6 spines at apex; outer apical lobe of hind tibia with apparently 3 (Fig. 18) indistinct spines situated far forward; subdiscoideus not interstitial.

Abdomen: Petiole arched at base, longitudinally strigose-granular dorsally; tergite (2-3) with a distinct area of weak granular or scaly-reticulate sculpture on about basal $3/8$, the remainder smooth; remaining tergites smooth, the sixth tergite obliquely tilted ventrally as seen from the side, giving the gaster a somewhat truncated apex in outline; ovipositor about $0.67\times$ FWL.

Color: Body color wholly testaceous except gaster beyond basal half of tergite (2-3) which is abruptly darker, light brown; eyes iridescent greenish-blue in white light; ocelli dark brown; antennae testaceous at base, becoming light brown apically; legs dark testaceous, the hind femora and tibiae slightly darker than the corresponding segments of the fore and middle legs; tibiae indistinctly lighter banded on about basal $1/4$; ovipositor sheath testaceous basally, becoming darker apically; fore wing infumated with two light brown transverse bands separated by a hyaline band through the basal $1/3$ of the stigma, the apex also hyaline; veins and apical $2/3$ of stigma light brown.

Variation: Paratype females. Little variation in sculpture intensity or color occurs, except that occasionally the middle $1/3$ of tergite (2-3) may show faint sculpture traces; number of spines on the fore tibia varies from 12-26; number of scutellar furrow cross carinae varies from about 4-8; spines on the outer apical lobe of the hind tibia are sometimes inconspicuous and occasionally apparently absent. Variation in other measurements and ratios given in Table 4.

Paratype males: Essentially parallel the variation in the females, except that the tarsi are comparatively shorter, about $3/4$ as long as their respective tibiae, and the sculptured area at the base of tergite (2-3) extends usually to about the mid-point of the tergite.

Paratypes: 8♀♀, 4♂♂, same data as holotype [USNM]. North Carolina: Tryon, 3♀♀, 4♂♂ [no date], Hopkins No. 3634d (W. F. Fiske) [USNM]. South Carolina: Yorkville, 1♀, 9 July 1913, Juniperus, Hopkins No. 9194q (J. E. Smith) [USNM].

Remarks: The paratypes are all reared from red cedar (Juniperus virginiana). In addition, I tentatively include in this species two series from Rye, New Hampshire (Hopkins Nos. 3512 and 3513b) reared from northern white cedar (Chamaecyparis thyoides) which agree with the paratypes in all characters except the ovipositor length which is distinctly longer and not overlapping ($0.94-1.02\times$ FWL versus $0.50-0.72\times$ FWL in red cedar reared material). Also, those from Chamaecyparis average slightly more flagellomeres (25-28 versus 20-26). Also, I include four females reared from arborvitae (Thuja occidentalis) (Hopkins No. 3751), whose ovipositors are intermediate (OSL/FWL $0.67-0.83$) and two short series with ovipositors about 0.50 FWL from bald cypress (Taxodium distichum) (Hopkins Nos. 1239b and 3378d). In all other characters, measurements and ratios, this material shows no distinctive differences, and all are parasitic on Phloeosinus species infesting conifers belonging to the families Cupressaceae and Taxodiaceae. Additional reared series from Thuja, Chamaecyparis and Taxodium are needed to determine whether the differences cited are real or representative of the extremes of a continuum.

The distinguishing characters of this species are the combination of the relatively narrow vertex and temples (see Table 4); iridescent eyes; two well-developed sub-parallel longitudinal carinae where the notauli converge; the darker gaster beyond the yellowish basal half of tergite (2-3); and the presence

of but 2-3 poorly developed (often inconspicuous) spines (Fig. 18) situated well anteriorly on the outer apical lobe of the hind tibia. Spathius impus appears most closely related to S. parvulus and S. pallidus.

The name is an arbitrary combination of letters.

Distribution: Probably widespread over the range of its host trees, in eastern North America. In addition to the paratype localities, I have seen specimens from Massachusetts, Michigan, New Hampshire, New York, Virginia, West Virginia, Florida, Louisiana, and Ottawa, Canada.

Hosts: I have seen several series from red cedar whose host is recorded as either Phloeosinus sp. or P. dentatus (Say) (Scolytidae), under Hopkins Nos. 2590a, 2591a, 2723d, h, i, j and k, 2884f, 3634d, 3639b, 6136a, 6412, 6493a, 6954, and 10762a. Material from white cedar which I provisionally include in this species (see Remarks) is recorded as reared from Phloeosinus sp. or P. canadensis Swaine, under Hopkins Nos. 3512, 3513b, 3751, and 3751b. The few specimens I have from bald cypress from southern U. S. are reared from Phloeosinus sp. under Hopkins Nos. 1239b and 3378d.

Hopkins' (1892) record of Phloeosinus graniger (= dentatus) in red cedar as a host of Spathius canadensis almost certainly belongs to this species, although I was unable to locate the specimens, which according to his original manuscript are labeled with number 2932. Also, Schedl's (1932) and Beal and Massey's (1945) records of Spathius tomici parasitic on the above hosts (and subsequent references to these records listed in Bushing, 1965) should be changed also to this species, as I have seen their respective reared series.

15. Spathius comes, new species

(Fig. 31)

Holotype. - female, Wisconsin: Neopit, 7-31-39, Hopk. U. S. 32852n, Lot No. 39-18515 ex. Melanophila fulvoguttata (H. C. Secrest) [USNM Type No. 70505].

Description of type female: Body length, 5.0 mm; FWL, 3.9 mm; ovipositor sheath length, 4.9 mm. Other measurements and ratios in Table 4.

Head: Flagellomeres 36; face strongly transversely strigose; frons with strong transverse striae, whose extremities are gently curved ventrally; vertex transversely strigose of uniform intensity from ocellar triangle to occipital carina, and becoming granular laterally at eyes; temples posteriorly strigose like vertex but becoming smooth along eye margin and at malar space; ocellar triangle slightly raised and delicately transversely strigose.

Thorax: Lateral areas of prothorax weakly developed with irregular diagonal cross carinae merging posteriorly into horizontally wrinkled to granular sculpture of remainder of propleuron; pronotum with a distinct shallow pit dorsally immediately anterior to the mesonotal margin; notauli shallowly crenulate anteriorly, converging into a broad, shallowly depressed rugose area; mesonotum abruptly declivous to pronotum, the lobes evenly granular; scutellar furrow about as broad as distance between lateral ocelli, and crossed by 7 variously developed carinae which converge slightly anteriorly; scutellum broad, weakly convex, the disc evenly granular; mesopleural disc predominantly horizontally finely striate-granular dorsally to granular above sternaulus; sternaulus relatively broad and shallow, crossed by about 17 delicate carinae which fan out slightly dorsally and quickly fade into the granular sculpture, except posteriormost elements which continue and gently arch posteriorly to mesocoxal cavity; prepectal carina complete; prepectal area with surface irregu-

larity and numerous setae; basal carina of propodeum and its forks mostly obscured by strong rugosity; costulae and carinae bounding area petiolaris distinct and well developed but with numerous irregular short branches; dorsal areas coarsely granular to rugose; lateral faces of propodeum rugose; areola and area petiolaris rugose; fore tibia with 28 spines arranged in irregular rows of two and with a row of 7 spines at apex; outer apical lobe of hind tibia with a row of 3 spines situated anteriorly; hind coxae subglobular, coarsely granular with weak oblique striation medially and dorsally; subdiscoideus not interstitial; mediella with a very short third abscissa.

Abdomen: Petiole about as long as middle tibia, stout and moderately arched basally; petiole sculpture dorsally predominantly rugose, becoming irregularly longitudinally striated apically; epipleurite of petiole extending to about petiole mid-point; tergite (2-3) with basal $13/32$ weakly granular to scaly-reticulate, the remainder of the tergite smooth and shining; lateral margin of tergite (2-3) thickened on about basal $1/2$; tergites 4 to 8 appearing smooth and shining, but with very faint sparse punctulation anterior to setal rows revealed at high magnification under proper light, this becoming progressively stronger apically, tergites 7 and 8 quite obviously punctulate-granular; ovipositor broadly curved and nearly as long as body.

Color: Head light orange-brown, the lower face and malar area weakly suffused with dirty yellow; prothorax, mesonotum and scutellum light ferrugineous; propodeum and mesopleura dark ferrugineous; petiole basally dark ferrugineous, apically suffused with bright orange-brown; gaster shining ferrugineous, tergites each with a lighter transverse subcuticular band anterior to setal row and sternites heavily suffused with dirty yellow; trochanters, maxillary and labial palpi and fore and mid coxae stramineous; antennae, tegulae and hind coxae and remainder of fore and middle legs testaceous, except all tibiae distinctly light banded on about basal $1/4$; hind femora and tibiae light ferrugineous; ovipositor sheaths ferrugineous to brown; fore wings infumated and distinctly banded as in Figure 31; basal third of stigma stramineous, remainder brown; costal vein testaceous, remaining veins light tan.

Variation: Paratype females. Variation in gaster color ranges from wholly ferrugineous to nearly castaneous, the subcuticular bands often obscure; basal $1/2$ of tergite (2-3) is often lighter, suffused with bright orange-brown; also, lower half of mesopleura (including sternaulus) may be lighter than remainder of thorax; number of fore tibial spines varies from 17 to 28 with a row of 6-8 at apex; sculpture intensity of mesopleural disc, base of tergite (2-3) and vertex is less strong on smaller specimens; propodeal carinae usually are partially obscured as in type, but if apparently distinct, never thick and prominent; scutellar furrow carinae variously developed, sometimes somewhat wrinkled and irregular; variation in measurements and ratios given in Table 4.

Paratype males: Variation tends to parallel that of females except that margin of most gastral tergites is thickened laterally.

Paratypes: 7♀♀, 2♂♂, same data as holotype except 8 emerged 22 Aug. 1939 and are labeled Hopk. No. 32852₀ [USNM]. Canada, Ontario: Waubamic, 2♀♀, 1♂, 2, 6 & 7 July 1915 (H. S. Parish) [CU]. U. S. A., New Hampshire: Durham, 4♀♀, 5♂♂, [May-June 1905] Hopk. U. S. 3516c1 and 3516c2, Tsuga bred (W. F. Fiske) [USNM]; Rye, 1♀, 1♂, 1 July 1905, Hopk. U. S. 3512f, Chmcyprs thyoides bred (W. F. Fiske) [USNM]. Ohio: Mentor, 2♀♀, 1♂, 15 May 1932, reared from hemlock borer (J. S. Houser) [USNM]. Pennsylvania: Hummelstown, 2♀♀, Hopk. U. S. 15399c, ex. Melanophila fulvoguttata in Tsuga canadensis (J. N. Knull) [USNM]. Wisconsin: Sawyer Co., 2♀♀, 4 & 30 June 1955, ex. Melanophila fulvoguttata (Hussain) [RDS].

Remarks: This species superficially resembles Spathius simillimus Ashmead (see also "Remarks" under S. simillimus). It may be distinguished from simillimus by the much longer ovipositor, absence of a well developed punctulate band anterior to the transverse row of setae on tergites 4-6, and by the narrower, less strongly granular vertex. Also, S. simillimus tends to have all propodeal carinae very thick and distinct, which is never true in S. comes.

Five females in the Porter collection from Hudson, Maryland, which differ in their longer ovipositor (about 1.7x FWL), more flagellomeres (39-43) and uniformly horizontally strigose mesopleural disc are tentatively included here until additional material is available.

Distribution: Probably widespread throughout eastern North America. In addition to the paratypes, I have seen specimens from Quebec, Nova Scotia, New York, Maryland, and West Virginia.

Hosts: Most of the reared specimens before me were bred from the buprestid Melanophila fulvoguttata (Harr.) in hemlock. Exceptions are the paratypes from Rye, N. H. (Hopk. No. 3512f) labeled as reared from Chamaecyparis thyoides (white cedar) from the scolytid Phloeosinus sp. This seems possibly a labeling error, since a long series with the same labels but Hopkins Nos. 3512 and 3512b belong to S. impus sp. n. which is commonly parasitic on Phloeosinus in red and white cedar.

Hopkins (1892, 1899) records the cerambycid Chrysobothris pusilla Cast. in spruce as a host for Spathius simillimus; this should be changed to S. comes, as the specimens (nos. 2557 and 2579, see "Remarks" for simillimus) properly belong to this new species.

16. Spathius benefactor, new species

Holotype. - female, New York: Lowr. Westchester Co., Reared elm sect.

22-27 May 1934 (A. P. Jacot) (letter 8-11-34) [USNM Type No. 70506].

Description of type female: Body length, 3.4 mm; FWL, 2.6 mm; ovipositor sheath length, 2.25 mm. Other measurements and ratios in Table 6.

Head: Flagellomeres 25; face transversely strigose and somewhat shining, becoming weakly rugose at malar spaces; frons delicately transversely striate; vertex faintly transversely strigose and shining, becoming smooth at eyes; temples posteriorly faintly wrinkled, more or less parallel to occipital carina, becoming smooth at eyes and malar spaces; ocellar triangle weakly raised and delicately strigose-granular; malar space slightly less than 1/2 eye height.

Thorax: Lateral areas of prothorax distinct anteriorly and narrow, with 3 or 4 oblique cross carinae, losing definition posteriorly in the predominantly horizontally strigose sculpture of the propleura; notauli narrow and shallowly crenulate anteriorly, meeting in a moderately depressed weakly rugose area from which 2 short posterior carinae emerge which extend to the posterior margin of mesonotum; mesonotum moderately declivous, the lobes evenly granular; scutellar furrow with 4 or 5 straight cross carinae; scutellum very weakly convex, the disc evenly granular; mesopleural disc smooth and shining above sternaulus, becoming weakly strigose posteriorly and longitudinally wrinkled dorsally below wings; sternaulus moderately impressed with about 12 ill-defined cross carinae, the most posterior elements apparently continuing and curving posteriorly to mesocoxae; mesosternum smooth, shining; prepectal carina complete; prepectal area smooth with weak irregular surface rugosity and sparse short setae; propodeal carina distinct but somewhat irregular, strongest and

best defined on posterior half of propodeum posterior to the insertion of the costulae; dorsal areas granular to weakly rugose in vicinity of basal forks and costulae; basal carina delicate and irregular, shorter than its forks which are also delicate and somewhat dissected with numerous short side branches; costulae strongest and best defined at junction with basal forks, becoming dissected and losing definition laterally; areola elongate, ill-defined anteriorly and enclosing weaker, somewhat reticulate rugosity; fore tibia with 20 spines arranged in an irregular single to double row and a row of 7-8 spines at apex; outer apical lobe of hind tibia with a row of 5 or 6 spines at apex; hind coxae sub-globular, granular to weakly obliquely striate dorsally; subdiscoideus vein not interstitial.

Abdomen: Petiole strongly longitudinally strigose dorsally, becoming somewhat reticulate rugose basally; tergite (2-3) with distinct area of granular to scaly-reticulate sculpture on about basal $2/5$ followed by a very narrow smooth space and then very much weaker central scaly-reticulation ending before the transverse row of setae, the apical margin smooth; lateral margin of tergite (2-3) weakly thickened at base; remaining tergite with transverse bands of sparse punctulation anterior to the transverse row of setae on each tergite, the 7th and 8th tergite with a somewhat more strongly shagreened sculpture, especially laterally; ovipositor $0.87\times$ FWL.

Color: Body color basically shining ferrugineous, except the pronotum, the lower half of the mesopleura and apex of the petiole to about middle of tergite (2-3) lighter, suffused with rufo-testaceous; antennae testaceous, becoming darker apically; maxillary and labial palpi stramineous; coxae and trochanters light to dark testaceous, the hind coxae darkest; femora and tibiae shining dark testaceous to ferrugineous, the hind darkest, the tibiae with a distinct lighter band on about basal $1/4$; tarsi typically testaceous, the last tarsomere slightly darker; eyes light gray with an iridescent greenish hue in white light; fore wings with two broad infumated bands separated by a hyaline transverse band through the basal $1/3$ of stigma; veins tan to stramineous.

Variation: Paratype females. Distinct transverse bands of sparse punctulation on the gastral tergites occur in about half of the specimens examined, although their visibility often depends largely on whether the tergites are sufficiently distended to expose the area anterior to the setae; the middle area of tergite (2-3) after the basal sculpture is typically smooth or at most weakly scaly-reticulate as in type; the area of sculpture at the base of tergite (2-3) is always present but sometimes very weakly developed; vertex sculpture varies from apparently smooth to well developed transverse strigosity; the mesopleural disc is nearly always smooth immediately above sternaulus but sometimes scaly-reticulate; sternaulus is typically expressed as in the type but sometimes is very shallow and obscure, and rarely is sharply infolded as a deep groove; the form of the propodeal carinae is typically as in type, but the basal carina and its forks vary from sharply defined to almost completely obscured; body color varies from dark testaceous to dark ferrugineous, but is typically shining light ferrugineous with the apex of the petiole to about the middle of tergite (2-3) lighter rufo-testaceous; the lower half of the mesopleura and the pronotum may or may not be lighter than the remainder of thorax; number of fore tibial spines varies from 12-30 with a row of 5-9 spines at the apex; the outer apical lobe of the hind tibia has from 3-6 spines but typically 4 or 5; variation in other measurements and ratios is given in Table 6.

Paratype males: Essentially parallel the same sorts of variation in sculpture and color noted for the females, except that area of sculpture on base of tergite (2-3) typically covers about basal $1/2$ of tergite, the lateral margins of

at least the anterior tergites are thickened, and the areola is usually slightly smaller than on the females, with the basal carina thus often longer than its forks.

Paratypes: 5♀♀, 9♂♂, same data as holotype [USNM, CU]. Canada: Quebec: Berthierville. 9♀♀, 2♂♂, 6 Aug. 1946 (A. Robert) [Montreal, CNC]. Massachusetts: Berkshire Co., Williamstown, 7♀♀, 8♂♂, 1 July 1965 [MCZ].

Remarks: Since Kaston and Becker's (1936) paper, the name *Spathius canadensis* Ashmead has come to be applied almost automatically to any *Spathius* reared from elm. However, detailed study of Ashmead's type (a female from Ottawa, Canada) and over 45 different series of *Spathius* from elm (resulting largely from the emphasis on Dutch Elm Disease research beginning in the mid-1930's) has convinced me that elm-reared *Spathius* belong to a single, undescribed species, and that *S. canadensis* is actually a senior synonym for *S. claripennis* and *S. tomici*. (See additional comments under the "Remarks" section of *canadensis*.) The type of *S. canadensis*, while having many similarities to *benefactor* in "gestalt", differs significantly in many respects, most notably by the type's relatively short ovipositor (0.54x FWL versus 0.62-1.09x FWL for *benefactor*), but also in its slightly greater ratios of IOD/EW and TW/EH and smaller ratio of OTW/OED.

In addition to the characters given in the key, *Spathius benefactor* is distinguished by the short malar space, always less than half of eye height, the typically wrinkled basal carina, greenish iridescent eyes and the typically smooth mesopleural disc above the sternaulus. Larger individuals are superficially similar to *S. laflammei*, but usually the combination of fewer flagellomeres (21-32 versus 29-42), fewer spines on the outer apical lobe of hind tibia (3-6, typically 4 or 5, versus 5-8 in *laflammei*, typically 6 or 7) and the narrower vertex of *benefactor* (see Table 6) will distinguish the two.

Biology: Under the name *canadensis*, this species has been investigated in some detail, particularly by Kaston (1937, 1939) and Robert (1951a & b, 1961); the life stages are figured by Kaston (1937, 1939) and Robert (1961). Kaston's drawing is reproduced in Clausen (1940) and Craighead (1950). Snodgrass (1941) has figured the male genitalia.

Kaston has studied the biology of this species' parasitism of the elm bark beetle *Hylurgopinus rufipes*, and Robert discusses it on three species of weevils (*Magdalis barbata*, *M. armicollis* and *M. inconspicua*) based on large samples over a four year period. The work of both can be summarized as follows: *Spathius benefactor* has two, perhaps as many as four, generations per year, a complete cycle requiring 5-6 weeks; at least two generations can be reared on the same population of weevils. It overwinters in the prepupal stage, transforming to the pupa in early May, the adults eclosing in late May. The sex ratio in the Quebec populations (Robert, 1960) was weighted in favor of the males, females never comprising more than 30-40% of the populations. Kaston states that this species attacks only the ultimate and penultimate instars, usually parasitizing only 5-10% (seldom more than 25%) of the beetle population. Robert records average levels of parasitism of 7.7-15.3% over the period 1947-1950, the highest recorded level being 57.7% at one locality in 1948.

Distribution: Throughout eastern North America north of North Carolina. I have seen several hundred specimens, representing Connecticut, Illinois, Kansas, Maryland, Massachusetts, Michigan, Minnesota, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Vermont, Virginia, Wisconsin, and Ottawa and Quebec.

Hosts: Of the hosts formerly recorded from *S. canadensis* (see Bushing,

1965), the following should be transferred to this species: Hylurgopinus rufipes, Scolytus multistriatus, S. rugulosus, Magdalis barbata, M. armicollis and Leperisinus aculeatus. (For the status of the others, see under "Hosts" of Spathius canadensis as herein defined.) The only additional record is Magdalis inconspicua Horn (Robert, 1960) from elm.

17. Spathius laflammei Provancher

(Fig. 23)

Spathius laflammei Provancher, 1880, Naturliste can. 12: 164, fig. 12. [Type locality: Unknown, probably near Quebec City, Canada (lectotype female in Laval Univ., Quebec)].

Females: Body length, 3.5-6.1 mm; FWL, 3.0-4.7 mm; ovipositor sheath length, 2.0-3.9 mm. Other measurements and ratios in Table 6.

Head: Flagellomeres 29-42; face coarsely transversely strigose; frons with strong transverse striation; vertex typically with weak transverse striation anteriorly behind ocelli, this quickly diminishing in intensity, the posterior half smooth and shining; temples nearly smooth, with weak rugosity posteriorly paralleling the occipital carina; ocellar triangle slightly raised and finely granular.

Thorax: Lateral areas of prothorax moderately developed with several oblique cross carinae, becoming obscured posteriorly in strong longitudinal strigosity of remainder of prothorax; notauli deep and crenulate anteriorly, meeting in a broad moderately depressed rugose area; mesonotum robust and abruptly declivous, the lobes evenly granular; scutellar furrow with 4-9 well developed straight cross carinae; scutellum broad, somewhat projecting, the disc granular, becoming weakly rugose at posterior margin; mesopleural disc typically smooth and shining above sternaulus (occasionally weakly scaly-reticulate), abruptly becoming longitudinally rugose dorsally and granular posteriorly; sternaulus well impressed, broad with several distinct cross carinae, the posterior elements continuing and curving posteriorly to meso-coxal cavities; prepectal carina complete; prepectal area more or less smooth; propodeal carinae often irregular or obscured in reticulate rugosity anteriorly, best defined on posterior portion of propodeum; dorsal areas coarsely granular to reticulate-rugose; basal carina obscured to irregularly wrinkled, slightly shorter than its forks which are also irregular and dissected with numerous short reticulate side branches; areola longer than broad, often poorly defined anteriorly and usually enclosing weak reticulate rugosity; fore tibia with 24-47 spines arranged in irregular row of two and occasionally three, and a row of 7-11 spines at apex; outer apical lobe of hind tibia with a row of 5-8 conspicuous spines (Fig. 23), typically 6 or 7; subdiscoideus vein not interstitial.

Abdomen: Petiole stout, reticulate rugose to longitudinally strigose dorsally; tergite (2-3) with distinct area of granular sculpture on about basal $1/3$ to $2/5$, the remainder of the tergite usually smooth, shining, but occasionally with faint sculpture on middle of tergite anterior to the transverse row of setae; remaining tergites each typically with a well developed transverse punctulate band anterior to the setal row, this sometimes obscured or covered by the overlapping margin of the previous tergite, the 7th tergite often shagreened dorsally; ovipositor 0.61-0.89x FWL.

Color: Body color typically ferrugineous, but varying from dark testaceous to nearly piceous, the head and apex of petiole to basal half of tergite (2-3)

lighter and the gaster beyond the basal half of tergite (2-3) darker, especially on darker individuals; coxae, trochanters and tarsi light testaceous, the hind coxae darker; femora and tibiae dark testaceous, usually nearly concolorous with thorax, the hind legs slightly darker; antennae dark testaceous, becoming darker apically; eyes gray, sometimes with a greenish iridescent hue in white light; ovipositor sheaths testaceous at base, becoming dark brown apically; fore wings with two broad dark transverse bands separated by a hyaline band through the base of stigma.

Males: Essentially agree with the females but often much smaller (2.0-4.5 mm), with as few as 20 flagellomeres, and the vertex is usually completely smooth and shining; sculpture on the base of tergite (2-3) usually covers about the basal half of the tergite and lateral margins of the tergites are thickened.

Remarks: *Spathius laflammei*, described in 1880, has always been poorly known, and no host records are reported. Although Ashmead (1893) included *S. laflammei* in his key, his concept of the species was based on something other than the type, and instead his characterization of it agrees exactly with the new species, *S. stigmatus* (see "Remarks" under that species). Through the courtesy of Dr. René Béique of Laval University, Quebec, I have been able to examine Provancher's type and compare it with other specimens. The type is a pinned female and bears a yellow label with the printed number 563; beneath that is a handwritten label "*Spathius laflammei* Prov." followed by a red lectotype label by P. M. Marsh, Feb. 1965. The fore tarsi, both middle legs and the right fore wing of the lectotype are missing; the remaining wings are very dirty and folded together. (For additional notes on Provancher's type, see Gahan and Rohwer, 1918, and Shenefelt, 1968.)

I tentatively include here several very flattened individuals which at first look quite different, their profile resembling that of *S. calligaster* (Fig. 17). They agree with the typical *S. laflammei* in sharing the broad, nearly smooth vertex and temples, but differ in the thorax shape, with the mesopleural disc usually scaly-reticulate to granular, and the body size is smaller (ranging upwards from 2.8 mm), with correspondingly fewer flagellomeres and shorter wings and ovipositor. All are in the U. S. National Museum collection, reared from hickory under Hopkins Nos. 1418a, 3649f, 3653e & f, and 10938c.

Diagnosis: This is a relatively large and robust species apparently related to *S. simillimus* and *S. floridanus*, sharing the relatively broad vertex and temples. It may be distinguished from them and from the other Nearctic species by the smooth mesopleural disc immediately above the sternaulus, almost smooth vertex and temples, and the greater number of spines on the outer apical lobe of the hind tibia (Fig. 23) (6-8 spines, versus 4-6 on *simillimus* and 2-4 on *floridanus*).

Distribution: Apparently widespread through eastern North America south to North Carolina. I have seen about fifty specimens, representing Connecticut, Kansas, Maryland, Massachusetts, Michigan, New Hampshire, New Jersey, New York, North Carolina, Rhode Island, Virginia, Wisconsin and Quebec, Canada.

Hosts: No hosts were previously recorded. I have seen several specimens reared from hickory (*Carya* spp.), all of which, where known, are reported as parasitic on the weevil *Magdalis olya* under the following Hopkins numbers: 3262c, 3528x1b, 3605d, 3649a, 3654d and 10761y. Also I have seen a single male labeled "ex *Eucrada humeralis*" (Anobiidae), and a series labeled "bred from beech" (AMNH).

18. Spathius trifasciatus Riley

(Figs. 15, 29)

Spathius trifasciatus Riley 1873, Rep. Insects No. 5: 106. [Type locality: Missouri: St. Louis (C. V. Riley) (allotype male in ANSP - not USNM Type No. 2764, see Remarks)].

Spathius unifasciatus Ashmead 1893, Can. Ent. 25: 70, 72. [Teste Muesebeck and Walkley, 1951, Agriculture Monogr. 2: 170. Type locality: West Virginia: Morgantown (holotype female in USNM, Type No. 2149)].

Females: Body length, 3.0-6.5 mm; FWL, 2.3-4.4 mm; ovipositor sheath length, 2.0-4.9 mm. Other measurements and ratios in Table 5.

Head: Antennae about as long as body; flagellomeres 25-36; face transversely strigose-granular; frons transversely striate, the central portion becoming irregularly rugose in large individuals; ocellar triangle usually distinctly raised and transversely striate; vertex delicately striate anteriorly, the intensity quickly diminishing posteriorly to become smooth and shining at occipital carina; temples delicately strigose more or less parallel to occipital carina, the intensity strongest adjacent to occipital carina and diminishing anteriorly toward eye and ventrally toward malar space which is smooth.

Thorax: Prothoracic lateral areas poorly defined, shallow, weakly crenulate anteriorly, merging posteriorly into the strongly developed predominantly horizontal strigose sculpture covering remainder of propleura; notauli deep and crenulate anteriorly, converging into a strongly depressed rugose area from which usually emerge two or three distinct short carinae which reach posterior margin of mesoscutum; mesonotum broad, moderately declivous, the lobes evenly granular; scutellar furrow deep, crossed by 5-8 strong carinae; scutellum moderately convex (but usually less so than in S. brunneus), the disc evenly granular and sides strongly obliquely striate; mesopleural disc longitudinally strigose to granular in smaller individuals, dorsally the striae become progressively stronger to reticulate-rugose on the anterior-dorsal region; sternaulus depressed, bordered below by a well developed gently curved longitudinal carina extending the length of the mesopleuron from the prepectal carina to the mesocoxal cavity and with several irregular oblique cross carinae above which curve dorsally and posteriorly; prepectal carina complete, strong; prepectal area sparsely punctate with hairs to apparently smooth; propodeal carinae development variable, the carinae usually partially obscured by the reticulate-rugose sculpture which predominates; basal carina usually much shorter than its forks; areola and area petiolaris usually confluent and slightly concave, more or less dominated by reticulate-rugose sculpture; dorsal areas granular basally, becoming reticulate-rugose in region of costulae and basal forks; fore tibia with 27-38 spines arranged in irregular rows of 2 or 3 and a row of 6-9 at apex; outer apical lobe of hind tibia with a row of 6-10 spines; hind coxae granular to obliquely striate dorsally and angled basally below; tegulae mostly finely granular; subdiscoideus not interstitial, arising above middle of brachial cell; first intercubitus almost always distinctly longer than second radial abscissa.

Abdomen: Petiole dorsally longitudinally strigose at apex to reticulate-rugose basally; tergite (2-3) usually with about basal 1/3 to 1/2 delicately scaly-reticulate, the remainder smooth or with punctulation laterally anterior to setae row (occasionally punctulation extends completely across tergite as a band in very large specimens); remaining tergites with narrow transverse punctulate

to weakly granular bands anterior to the setae row, these bands variously developed, but strongest laterally, the central portions sometimes obscured and often not visible due to the overlapping margin of previous tergite; epipleurites weakly punctulate; gastral sculpture intensity seems to vary according to individual size, smaller specimens having gasters which appear nearly smooth; margin of tergite (2-3) weakly thickened at base.

Table 5. Measurements and ratios of selected characters for females of the trifasciatus species group. Top line in each instance gives range; number below brunneus is for lectotype; trifasciatus holotype lost.

	<u>trifasciatus</u>	<u>brunneus</u>
n	13	11
number of flagellomeres	25-36	31-34 broken
body length (mm)	3.0-6.5	2.9-4.9 4.5
FWL (mm)	2.3-4.4	2.7-3.8 3.6
MS/EH	0.44-0.53	0.43-0.55 0.49
TW/EH	0.64-0.95	0.69-0.81 0.74
IOD/EH	1.02-1.24	1.00-1.14 1.09
OTW/OED	0.72-1.00	0.67-0.82 0.74
OED/OOD	0.60-0.78	0.59-0.70 0.63
Pet. L/(2-3)L	1.11-1.61	1.35-1.65 1.35
ICu ₁ /R ₂	0.92-1.42	0.97-1.04 1.03
OSL/FWL	0.87-1.20	0.45-0.68 0.50

Color: Body predominantly typically dark ferrugineous to piceous, except about apical half of petiole and about basal half of tergite (2-3), which are nearly always distinctly lighter, usually fulvous, light ferrugineous or yellow; head usually somewhat lighter than thorax; thorax with propodeum darkest, sometimes (along with base of petiole) nearly black, the prothorax, prepectal areas and lower mesopleura (sternauli) usually slightly lighter than dorsal parts (very

much lighter, stramineous, in one female from Mississippi); eyes usually an iridescent bluish-green in white light; flagellomeres dull ferrugineous to nearly brown; ovipositor sheaths brown, though slightly lighter basally; palpi, fore and mid coxae testaceous; hind coxae and all femora and tibiae dull ferrugineous, the hind darkest; tibiae with a distinctly lighter band on about basal $1/5$; fore wing distinctly banded as in Figure 29; basal third of stigma pale whitish yellow; veins pale brown to dull ferrugineous; tegulae light ferrugineous to testaceous.

Males: Agree with females in most morphological features except femora are much more swollen (Fig. 15) and margin of tergite (2-3) and most subsequent tergites is thickened laterally; also, number of spines on the fore tibia is fewer, ranging from 10-24 arranged in an irregular single to double row.

Remarks: In the U. S. National Museum are four pins of supposed S. trifasciatus Riley with red "USNM type no. 2769" labels catalogued by Ashmead in 1896: 2♀♀, 1♂, and 3 cocoons. In actuality, the adults represent not one but three species of Spathius: S. trifasciatus (♂), S. stigmatus, sp. n. (♀), and S. floridanus Ashmead (♀). Noting this error by Ashmead, Rohwer later affixed handwritten "Not Type. Roh." labels on the two females and "Spathius trifasciatus Riley Allotype male ? Roh." to the male specimen. However, it now appears that even this male is not the true allotype.

The source of Ashmead's confusion may possibly have been the three cocoons glued to a single point with the labels "21701" and "From Scolytus caryae" in Riley's handwriting. On file in the U. S. National Museum on 3x5 cards are excerpts from notes and letters of Riley; one card headed "No. 217R Scolytus caryae Riley" states "Bred a Bracon from it - See 5th Rept. Marked 217⁰ in Box 2, also a second one 217⁰¹ in Box 2. (Both sent to Cresson Mch 20/73)." I suspect that Ashmead somehow obtained the cocoons, discovered that the number matched that in Riley's notes, and proceeded to catalogue three specimens which he thought to have emerged from these cocoons without checking them further.

However, in 1873 Cresson was at the Philadelphia Academy, and among the Spathius which Dr. P. M. Marsh recently found there was a single male S. trifasciatus labeled "Mo." and "217⁰" with a third label "Par. Scolytus caryae" in Riley's handwriting. I have no doubt that this is the true allotype male. The female which should bear the label "217⁰¹" is apparently lost; it is definitely not in the U. S. National Museum and Dr. Marsh, in a subsequent trip to Philadelphia, has specifically searched for it, at my request, without success.

Still unexplained are how Ashmead came to have the cocoons and mismatched adults and why the cocoons were not mentioned by Riley in either his notes or original description. However, since Riley's description is based chiefly on the female and his original female specimen seems to be lost, one alternative would be to select a neotype female in addition to the positively identified allotype to henceforth stand as the name bearer for the species. Since there is always the possibility that the lost type female may eventually be found, I have decided not to select a neotype, but rather have labeled a female from Topeka, Kansas (USNM), as plesiotype so that subsequent workers will know the basis for my concept of S. trifasciatus Riley.

Additional evidence that Ashmead was confused as to the identity of Riley's S. trifasciatus is the fact that he described S. unifasciatus which has proved to be synonymous (teste Muesebeck and Walkley, 1951). I have seen Ashmead's type and agree that it is a synonym of S. trifasciatus. The type pin (USNM Type No. 2149) has both a male and female, though Ashmead mentions only

the female; however, the label number 3164 agrees with the Hopkins original manuscript for his 1892 paper. Interestingly, in his table of species, Ashmead separates *S. trifasciatus* and *S. unifasciatus* in two different parts of the key and states *S. trifasciatus* to have an ovipositor twice as long as its body, which is clearly an error. Unfortunately, this is but another indication of the haste with which he often worked.

Diagnosis: *Spathius trifasciatus* may be readily distinguished from its closest relative, *S. brunneus*, by the longer ovipositor, darker body color and the strongly depressed rugose area where the notauli converge.

Distribution: I have seen well over 100 females and at least 50 males, representing the following localities: Kansas, Maryland, Mississippi, Missouri, New Jersey, New York, North Carolina, Pennsylvania, Texas, Virginia, West Virginia and the District of Columbia. These suggest that the range of *S. trifasciatus* is eastern United States, south of a line from Massachusetts to Kansas and west to Kansas and Texas, except the extreme southeast. Probably the range will be found to mirror that of its host trees, hickory (*Carya* spp.), which occur throughout the deciduous forests of the eastern U. S.

Hosts: The first and most frequently recorded host in the literature is *Scolytus quadrispinosus* Say (= *S. caryae* Riley) in hickory. Numerous authors have cited this host and a summary of these may be found in Bushing (1965). In addition, Blackman and Stage (1924, p. 165-166) list *Magdalis olya* in hickory as a probable host, and Felt (1915, p. 29) reports it parasitic on the hemlock borer, *Melanophila fulvoguttata* Harr. In both cases, the evidence suggests that the parasite wasps were misidentified.

In the case of *Magdalis olya*, I have already cited the agreement between Blackman's specimen labels and his comments under *S. stigmatus* sp. n. In addition, Blackman and Stage state (p. 166) that "In not a single case was it [*S. trifasciatus*] found associated with *E. quadrispinosus* although the hickory bark beetle had emerged two years previously from the material in several of these cages." I can further add that no true *S. trifasciatus* were found among the material borrowed from the Syracuse University College of Forestry collection. The fact that one of the types catalogued as *S. trifasciatus* was *S. stigmatus* (see Remarks) suggests the possible source of error.

In the case of the *Melanophila* host record, I have not seen the reared specimens in question. However, the new species, *S. comes*, is reared from *M. fulvoguttata*, and in many respects superficially resembles *S. trifasciatus*. Also, none of the *S. trifasciatus* specimens before me are reared from hemlock. Therefore, I am inclined to doubt the validity of this host record.

The only other published host record is *Scolytus rugulosus* (Ratzeburg) (Chamberlin, 1939). Since I have no specimens which confirm this record, I am inclined to question its validity as well, especially since it is an introduced species and works primarily in *Prunus*, *Pyrus* and *Crataegus*, which are not particularly closely allied to hickory.

The available evidence suggests that *S. trifasciatus* is largely restricted to bark beetles (primarily *S. quadrispinosus*) and other borers in the various species of hickory, as originally reported by Riley and by Ashmead for *S. unifasciatus*. All reared specimens I have seen are from hickory (rarely oak), many recorded with associated insects in the Hopkins' card file at the U. S. National Museum under the following numbers: 3262c, 3458c, 6850c, 9423b3, 10764-c, 10935i, 10936b, 10937b, 10938c, 10938d. In addition I have seen the *S. unifasciatus* specimens referred to by Beal and Massey (1945) (from Durham, North Carolina, no. 1573) and can confirm their identity. Their additional reference to *S. unifasciatus* parasitizing *Hylurgopinus rufipes* is to be doubted.

19. Spathius brunneus Ashmead

(Fig. 14)

Spathius brunneus Ashmead 1893, Can. Ent. 25: 72. [Type locality: West Virginia: Morgantown (A. D. Hopkins) (lectotype female in USNM, Type No. 70507)].

Spathius bruneus [sic] Dalla Torre 1898, Cat. Hym. 4: 243.

Females: Body length, 2.9-4.9 mm; FWL, 2.7-3.8 mm; ovipositor sheath length, 1.4-2.6 mm. Other measurements and ratios in Table 5.

Head: Antennae about 1.5x FWL; flagellomeres 31-34; face transversely strigose-granular; frons finely transversely striate, becoming finely granular at eyes; vertex delicately transversely striate to nearly smooth, especially posteriorly adjacent to occipital carina; temples with delicate strigosity parallel to occipital carina, becoming finely granular toward eyes and smooth at malar space; ocellar triangle faintly granular to delicately transversely striate.

Thorax: Robust, about 0.7x as high as long (Fig. 14); lateral areas of prothorax shallow, narrow and smooth with about 9-12 oblique cross carinae, these losing definition posteriorly to become obscured by the horizontally strigose granular sculpture covering remainder of propleura; notauli shallowly crenulate anteriorly converging to a slightly depressed rugose area from which emerge usually two distinct carinae reaching posterior margin of mesonotum; mesonotum moderately declivous, broad, the lobes evenly granular; scutellar furrow broad, gently arched around anterior margin of scutellum and having 6-10 well developed evenly spaced cross carinae; scutellum strongly convex (Fig. 14), the disc evenly granular and sides obliquely striate; mesopleural disc centrally usually nearly smooth, becoming progressively granular, then with delicately swirled striations at outer limits of area and dorsally longitudinally strigose; sternaulus (Fig. 14) indistinct, smooth, and lacking cross carinae, instead bordered below by a strong gently curved longitudinal carina extending the length of the mesopleuron from the prepectal carina to the meso-coxal cavity, with up to 5 shorter, variously developed carinae more or less paralleling it above; prepectal carina complete, strong; prepectal area nearly smooth, sometimes with a few irregular oblique carinae extending from the anterior margin; propodeal carinae development variable, strongest posteriorly; basal carina weakly developed, usually shorter than its forks; areola and area petiolaris confluent, granular, crossed by several irregular carinae; costulae more or less perpendicular to basal forks; dorsal areas granular basally, becoming reticulate-rugose at costulae; fore tibia with 35-47 spines arranged in irregular rows of 2 or 3, and a row of 7-8 at apex; outer apical lobe of hind tibia with a row of 6-7 spines; hind coxae basally angled below, with indistinct oblique striations or weak granular sculpture dorsally; subdiscoideus not interstitial, arising above middle of brachial cell; tegulae basally faintly granular, apically smooth.

Abdomen: Petiole dorsally uniformly longitudinally striate at apex, becoming irregularly longitudinally strigose to reticulate-rugose at base; tergite (2-3) usually with a very weakly scaly-reticulate area on about basal 5/12, followed by a narrow smooth space and then by a narrow transverse band of sparse fine punctures immediately anterior to the subapical transverse row of elongate setae, the tergite smooth posterior to the setae row; tergites 4-7 each with similar transverse narrow punctulate bands just anterior to the setae row, these bands usually mostly covered by the overlapping margin of previous ter-

gite; ultimate tergite, when visible, appearing granular apico-laterally; variation in gastral sculpture often seems correlated with specimen size, *i.e.*, larger individuals show much more strongly developed punctulate bands and basal aciculation on tergite (2-3), while on smaller individuals the sculpture is often very faint, the gastral tergites appearing smooth; margin of tergite (2-3) weakly thickened at base.

Color: Body more or less uniformly testaceous except gaster beyond basal half of tergite (2-3), which varies from dull ferrugineous to castaneous; palpi stramineous to testaceous; antennae honey yellow to testaceous, the apical 10-15 flagellomeres becoming dusky brown; flagellomeres each with a very narrow darker apical band; eyes usually an iridescent bluish green in white light; mandible tips ferrugineous; legs testaceous, the tibiae, especially hind tibiae, sometimes slightly darker and always distinctly lighter on about basal $1/5$, appearing banded; ovipositor sheaths testaceous basally, apical half brown; fore wing distinctly banded very similarly to *S. trifasciatus* (Fig. 29); basal third of stigma and sometimes costa pale yellow, other veins usually pale brown; costula of hind wing usually pale yellow especially in area of hamuli; tegulae pale yellow to testaceous.

Males: Agree with females in color and most morphological features except femora are much more swollen and margin of tergite (2-3) and most subsequent tergites is thickened laterally; also gastral sculpture is usually reduced in intensity, the punctulate bands often completely obscured and the basal half of tergite (2-3) usually appearing smooth. Number of fore tibial spines is also reduced, ranging from about 24-30.

Remarks: As was true for several of the *Spathius* described in his 1893 paper, Ashmead gave no formal description of *S. brunneus* beyond that in his "Tables of Species". The specimen which surely represents the type bears the labels "179 Hopk. W. Va." and "*Spathius brunneus* Ashm. ♂, ♀, Ashm." in Ashmead's handwriting. A third label in S. A. Rohwer's handwriting says "Ashmead Type". Although Ashmead does not give a host record, the number 179 matches a number on Hopkins' original manuscript for his 1892 paper in which *S. brunneus* is reported parasitic on "*Scolytus muticus* (?) and *Agrilus fallax*". On the pin are two females and one male, each on a separate point. I have placed a red ink mark near the base of the point of the female having both flagella missing and here designate this female as the lectotype. The other female and male thus become paralectotypes. Since *S. brunneus* was not previously catalogued in the U. S. National Museum type collection, it has been designated USNM Type no. 70507.

Diagnosis: This species may be readily distinguished from its closest relative, *S. trifasciatus* Riley, by its lighter body color, shorter ovipositor, less strongly depressed notauli, more conical scutellum (Fig. 14), and lack of cross carinae on the sternauli.

Distribution: In addition to the type I have seen 12 females and 6 males, all in the U. S. National Museum collection. All are reared from *Celtis occidentalis* and represent three localities: Plummerville, Maryland; Mariana, Florida; and Morgantown, West Virginia, the type locality.

Hosts: Three hosts are recorded: *Scolytus muticus* Say, *Agrilus fallax* Say and *Scolytus ventralis* LeConte. The first two species were originally reported as hosts by Hopkins (1892), and one or both repeated in Hopkins (1893a and 1893b), Dalla Torre (1898), Pierce (1908), Chamberlin (1939) and Bushing (1965). *Scolytus ventralis* is apparently a copy error introduced by Chamberlin (1939) and repeated in Bushing (1965). Chamberlin cites Bedard (1938) as his source, but Bedard referred not to *S. brunneus* but to *Spathius brunneri* Viereck, a

known parasite of Scolytus ventralis. No additional host records have been found.

Table 6. Measurements and ratios of selected characters for females of the laflammei and simillimus species groups. Top line in each instance gives range; number below is for holotype or lectotype.

	<u>laflammei</u>	<u>benefactor</u>	<u>simillimus</u>	<u>floridanus</u>
n	10	23	12	14
number of flagellomeres	29-42 broken	21-32 25	27-33 27	23-39 broken
body length (mm)	3.5-6.1 4.7	2.2-4.3 3.4	2.9-4.5 3.3	1.4-4.6 4.0
FWL (mm)	3.0-4.7 3.8	1.9-3.4 2.6	2.5-3.4 2.8	1.9-4.2 4.1
MS/EH	0.48-0.63 0.63	0.41-0.50 0.46	0.44-0.50 0.50	0.47-0.67 0.48
TW/EH	0.67-0.77 0.77	0.55-0.74 0.57	0.57-0.67 0.62	0.64-0.85 0.67
IOD/EH	1.06-1.33 1.33	0.96-1.12 1.04	1.00-1.17 1.17	1.00-1.33 1.07
OTW/OED	0.72-0.89 0.73	0.75-1.07 0.86	0.69-0.86 0.71	0.64-0.88 0.84
OED/OOD	0.58-0.78 0.73	0.71-0.88 0.78	0.61-0.73 0.70	0.56-0.78 0.59
Pet. L/(2-3)L	1.36-1.77 1.52	1.39-2.00 1.53	1.25-1.70 1.42	1.10-1.61 1.47
ICu ₁ /R ₂	0.90-1.20 1.14	0.91-1.25 1.04	0.84-1.25 1.15	0.88-1.35 1.00
OSL/FWL	0.61-0.89 0.66	0.62-1.09 0.87	0.58-0.78 0.64	0.65-1.10 0.98

20. Spathius simillimus Ashmead

Spathius simillimus Ashmead, 1893, Can. Ent. 25: 70, 73. [Type locality: West Virginia: Morgantown (lectotype female in USNM, Type No. 2150)].

Females: Body length, 2.9-4.5 mm; FWL, 2.5-3.4 mm; ovipositor sheath

length, 1.6-2.4 mm. Other measurements and ratios in Table 6.

Head: Flagellomeres 27-33; face coarsely granular; frons strongly transversely strigose medially, giving way to granular sculpture at eyes and ocelli level; vertex relatively broad, OOD distinctly greater than OED and TW, vertex prominently and completely uniformly granular with only weak indication of transverse strigosity, this extending to frons, eyes, and continuing onto temples nearly to malar space; malar space not more than half of EH; ocellar triangle granular, weakly raised.

Thorax: Lateral areas of prothorax indistinctly defined, more or less obscured posteriorly by the generally rugose to coarsely granular sculpture of remainder of prothorax; notauli strong, crenulate anteriorly, meeting in a broad slightly depressed area of strong rugosity; mesonotum abruptly declivous, the lobes uniformly granular; scutellar furrow narrowest at mid-point, broadening laterally and crossed by 6-9 variously developed, often wrinkled irregular carinae; scutellum weakly conical, the disc granular, becoming weakly rugose at posterior margin; mesopleural disc evenly granular to scaly reticulate immediately above narrow sternaulus, giving way to stronger longitudinal strigosity dorsally; mesosternum below sternaulus also evenly granular to scaly-reticulate; sternaulus a narrow moderately impressed furrow, very slightly broader posteriorly and crossed by several variously developed, usually irregular carinae which end abruptly above, never continuing posteriorly or onto mesopleural disc; prepectal carina complete; prepectal area more or less smooth with weak surface irregularity and sparse setae; propodeal carinae prominent, very thick and always well developed, especially the basal carina and its forks; dorsal areas coarsely granular to weakly rugose; basal carina usually slightly shorter than its forks; costulae typically distinctly forked almost at base, the posterior branch extending to the posterior-lateral angles which are usually slightly projecting; areola an elongate trapezoid typically somewhat concave centrally and enclosing several irregular parallel transverse carinae; fore tibia with 16-26 spines arranged in irregular single to double rows and a row of 6-8 spines at apex; outer apical lobe of hind tibia with 4-6 spines, typically 5; hind coxae coarsely granular with weak oblique striation on the inner dorsal surface; subdiscoideus not interstitial.

Abdomen: Petiole typically robust, dorsally granular to longitudinally strigose apically and arched at base; tergite (2-3) always distinctly sculptured, approximately the basal 5/11 to 1/2 strongly granular followed immediately by a less strong or sometimes obscure granular to scaly-reticulate area on about next 3/11 to transverse row of setae, the apical 3/11 beyond the setal row always smooth; remaining tergites each with a well defined distinct transverse punctulate band immediately in front of the row of setae, the apical portion beyond the setal row smooth; punctulation extends onto the epipleurites but is much weaker; tergite (2-3) weakly thickened laterally at base; ovipositor slightly curved, 0.58-0.78x FWL.

Color: Body color basically dull to dark ferrugineous except that sternauli and lower half of mesopleura are often much lighter, typically testaceous and the basal half of tergite (2-3) and apical half of petiole are usually lighter, especially in darker individuals; also, the venter and the apex of the gaster tend to be lighter than the dorsum, often testaceous; eyes dark gray, with rarely any evidence of iridescence in white light; antennae testaceous, becoming darker apically; maxillary and labial palpi dark testaceous; coxae and trochanters testaceous, never as dark as body, the hind coxae usually slightly darker than the fore and mid coxae; femora and tibiae dark testaceous to ferrugineous, the tibiae distinctly lighter banded on basal 1/4 to 1/3; tarsi testaceous,

the ultimate tarsomere typically distinctly darker than others; fore wings darkly infumated with a distinct lighter transverse band medially and apically like floridanus (Fig. 3).

Males: Essentially agree with females in all important respects; number of flagellomeres varies from 23-32 and the lateral margin of most gastral tergites is thickened.

Remarks: According to the USNM Type Catalog (Type No. 2150), Ashmead had a total of 27 individuals of S. simillimus before him, including representatives of both sexes. Comparing the numbers on the labels with those on Hopkins' original manuscript for his 1892 paper, those determined as simillimus include numbers 3095, 3207 and 3262, all reared from Agrilus bilineatus living in white oak, and numbers 2557 and 2579 reared from an unknown host in Abies nigra and a buprestid larva in an unstated host. However, in his description, Ashmead does not note the latter hosts, stating simply, "Bred May 18 and 25, 1892, from Agrilus bilineatus living in White Oak stump." Also, the dates given agree only with numbers 3207 and 3262, respectively. Of four pins bearing these numbers (with a total of 12 specimens), only one also has a handwritten Ashmead label "Spathius simillimus Ashm." (No. 3262).

This background is important in order that the name simillimus may be properly and positively associated, since the 7 specimens on 4 pins labeled with numbers 2579 and 2557 belong not to simillimus, but to the new species, Spathius comes. I base my decision as to which should be called simillimus primarily upon Ashmead's statement of only the one host and the presence of his determination label on but one pin as noted above, since his description, with one exception, could apply equally well to either species. The exception is his statement "ovipositor as long or very little shorter than the body." This would apply only to comes which has a distinctly longer ovipositor (OSL/FWL 0.91-1.57) and not to simillimus as I define it (OSL/FWL 0.58-0.78). However, on the basis of the above evidence I choose to ignore this discrepancy and have selected as lectotype one of two females on one of the pins bearing number 3207, and have designated it by a red ink mark at the base of the point. All of the other specimens labeled with numbers 3207, 3095 and 3262 are thus labelled as paralectotypes.

Aldrich (1921) gives a figure of Spathius simillimus. A specimen of this species in the USNM bearing Hopkins No. 11254a has a label saying "type of drawing" and may be assumed to be the specimen on which the drawing was based.

Diagnosis: The presence of distinct transverse punctulate bands on all gastral tergites anterior to the setal row will usually distinguish this species from most other North American forms. The very well developed sculpture on the vertex and temples is also diagnostic, occurring in about equal development only on S. floridanus which has the gaster nearly smooth. The form of the sternaulus and mesopleuron is also distinctive, the carinae of the sternaulus rarely distinctly extending onto the uniformly granular to scaly-reticulate mesopleural disc or curving posteriorly to the mesocoxal cavity as in floridanus, comes or pallidus which may sometimes be confused with it.

Distribution: Probably widespread in eastern North America north of Virginia. However, as in the case of S. brunneus, I have seen only reared material, consisting of five series in all, and representing Maine, Massachusetts, Virginia, West Virginia and New Brunswick, Canada. In addition, Pennsylvania is listed (Muesebeck et al., 1951), Felt (1905) reports it from New York, and Chittenden (1897) notes its abundance in the District of Columbia. The reported occurrence of this species in Mississippi and Wisconsin

(Muesebeck, 1967) is possibly erroneous, as I have not seen material to support it.

Hosts: Recorded hosts that I have been able to confirm are the buprestids *Agrilus bilineatus* (Weber) and *A. anxius* Gory. The former was first recorded by Hopkins (1892) from white oak and has been repeated by the following: Ashmead (1893), Hopkins (1893b, 1899), Chittenden (1897), Dalla Torre (1898), Felt (1905), Viereck (1910), Muesebeck (1928, in Leonard), Doane et al. (1936), and Muesebeck and Walkley (1951). *Agrilus anxius* in birch was first reported as a host by Nash et al. (1951) and repeated in Muesebeck and Walkley (1951) and Barter (1957). Balch and Prebble's (1940) reference to *Spathius* sp. refers to this species, as I have seen their specimens (CNC).

Hopkins (1892, 1899) records two additional species as hosts: *Chrysobothris pusilla* Cast. (Cerambycidae) in spruce and the weevil *Cryptorhynchus ferratus* Say in sassafras. These are regarded as erroneous. The former is no doubt a record for the new species, *S. comes* (Hopkins manuscript numbers 2557 and 2559). The latter I am unable to substantiate or relate to any specimens I have seen.

Specimens of *S. simillimus* which I have seen bear Hopkins numbers 1717a, 11254 and 11847b. The first was reared from an unrecorded host in chestnut, the second from *Agrilus bilineatus* in chestnut and the last from the cerambycid *Callidium aereum* Newman in white oak, a new host record. Thus *Spathius simillimus* seems comparatively specific in its host preferences, attacking buprestid or cerambycid larvae in deciduous trees, especially birch and white oak.

21. *Spathius floridanus* Ashmead

(Figs. 1-3, 24)

Spathius floridanus Ashmead, 1893, Can. Ent. 25: 71. [Type locality: Florida: Jacksonville (holotype female in USNM, Type No. 52646)].

Females: Body length, 2.2-6.8 mm; FWL, 1.9-4.2 mm; ovipositor sheath length, 1.3-4.6 mm. Other measurements and ratios in Table 6.

Head (Figs. 1 and 2): Flagellomeres 23-39, face coarsely transversely strigose-granular; frons strongly transversely striate to rugose-granular, with at least the granular sculpture always extending to eyes; vertex relatively broad, OOD distinctly greater than OED (Fig. 24), and prominently and completely granular to transverse strigose-granular, extending undiminished to eyes, frons, and onto entire temple nearly to malar space; ocellar triangle weakly raised, granular.

Thorax: Lateral areas of prothorax variously defined, usually becoming obscured posteriorly in the longitudinal granular strigosity of remainder of propleura; pronotum dorsally broad with several fine slightly oblique transverse striations usually visible anterior to where the lateral areas converge; notauli deep, crenulate anteriorly meeting in a moderately depressed area of strong rugosity extending to the posterior margin of the mesonotum; mesonotum abruptly declivous, the lobes uniformly granular; scutellar furrow relatively broad with irregular variously developed cross carinae, these rarely simple and distinct but with various transverse connections and rugosity at least partially obscuring them; scutellum broad, moderately convex, the disc evenly granular, becoming weakly rugose at posterior margin; mesopleural disc variable, usually scaly-reticulate to nearly smooth anteriorly above sternau-

lus, this giving way to irregular weak more or less longitudinal rugosities immediately above posterior portion of sternaulus, with stronger longitudinal granular strigosity occurring more dorsally beneath the wings; sternaulus variously developed, from a very weak granular longitudinal impression to occasionally a sharply infolded steep-sided groove, but typically moderately impressed and crossed by several poorly developed, irregular carinae some of which may appear to extend weakly onto mesopleural disc or curve posteriorly towards mesocoxal cavities; mesosternum scaly-reticulate adjacent to sternaulus, to nearly smooth; prepectal carina complete; prepectal area more or less smooth with weak surface irregularity and sparse setae; propodeal carinae distinct, and sharply defined; dorsal areas granular to rugose; basal carina typically shorter than its forks, resulting in a relatively broad and elongate areola which typically encloses several weaker reticulate cross carinae; costulae well defined, angled somewhat anteriorly; area petiolaris small but bounded by very thick and prominent carinae laterally; fore tibia with 13-25 spines arranged in an irregular single to double row and a row of 5-9 at the apex; outer apical lobe of hind tibia with 2-4 spines, typically 3 situated somewhat anteriorly; subdiscoideus not interstitial.

Abdomen: Petiole moderately stout, arched at base, with granular irregular longitudinal strigosity dorsally; tergite (2-3) variable in degree of sculpture developed, from virtually smooth and shining with perhaps very faint traces of scaly-reticulate sculpture to distinct area of granular to scaly-reticulate sculpture on basal $3/8$ to $1/2$, rarely with any sculpture present beyond the basal half; remaining tergites typically smooth but larger individuals sometimes with weak indications of punctulate or faint scaly-reticulate transverse bands anterior to the setal row on some tergites; epipleurites usually very faintly punctulate; lateral margin of tergite (2-3) weakly thickened at base; ovipositor varies from 0.65-1.11x FWL.

Color: Body color typically light ferrugineous, but considerable variation exists from basically testaceous to dark ferrugineous, the gaster varying from entirely shining honey yellow to entirely dark shining ferrugineous or with the basal $1/2$ to $2/3$ of tergite (2-3) lighter than remainder of gaster or occasionally the gaster with two to four subcuticular narrow transverse ferrugineous bands; also the propodeum and petiole may be distinctly lighter than the gaster and remainder of thorax, or the propodeum, petiole and part or all of the gaster may be lighter than the remainder of the thorax; legs usually more or less concolorous with body or slightly lighter, especially the trochanters and tarsi; tibiae distinctly lighter banded on about basal $1/4$ - $1/3$; ultimate tarsomere usually at least slightly darker than preceding tarsomeres; antennae testaceous at base, gradually darkening apically; ovipositor sheaths testaceous basally, becoming darker brown apically; eyes typically gray, rarely with a faint iridescent hue in white light; fore wing (Fig. 3) distinctly banded and darkly infumated, veins and stigma (except lighter basal $1/3$) brown.

Males: Essentially parallel the variation in the females in sculpture and color, although smaller males often have the intensity of the sculpture somewhat reduced on the head and mesopleura; however, the most notable difference is in the amount and intensity of sculpture on tergite (2-3), which in males tends to regularly cover more than the basal $1/2$, often extending to the transverse setal row or over about $3/4$ of the tergite; also gaster color beyond the basal $2/3$ of tergite (2-3) is frequently much darker, to nearly piceous.

Remarks: This robust species, based on a single female, was never formally described beyond the characters given by Ashmead (1893) in his "Table of Species", and has heretofore been of uncertain status. In part, this was

due to its having been confused with *S. trifasciatus* Riley (see Remarks section under that species) and in part because the holotype is a large specimen and in some respects atypical for the species. In addition to the locality label, the holotype has a label "*Spathius floridanus* Ashm." in Ashmead's handwriting and the red "USNM Type No. 52646" label.

Diagnosis: This species is most closely related to *Spathius simillimus*, from which it may be most readily distinguished by the absence of well developed transverse punctulate bands anterior to the row of setae on each of the gastral tergites. In addition, the more rugose scutellar furrow, the usual presence of more or less longitudinal irregularity on the mesopleural disc immediately above the sternaulus, at least posteriorly (compared to the uniformly granular or scaly-reticulate mesopleural disc of *simillimus*) and the presence of fewer spines on the outer apical lobe of the hind tibia (typically 3, versus 5 in *simillimus*) will assist in distinguishing the two.

Distribution: Throughout eastern North America, from Florida to Ontario and Quebec, Canada, and west to Texas, Kansas and Minnesota. The over 300 specimens which I have seen represent nearly every state in this region.

Biology: *Spathius floridanus* appears to differ from the majority of the known *Spathius* species in that several individuals are usually reared from a single host larva. I reared four individuals from a cluster of cocoons in a cerambycid burrow under oak bark; a similar cluster of 9 cocoons is pinned with Hopkins No. 1460c, and another cluster of 7 cocoons is pinned with Hopkins No. 9909b'. Comments on the cards in the Hopkins file often state "ex mass of parasite cocoons in larval mines." In each of the above three cases, the reared adults include both sexes, suggesting that this is probably a case of multiple oviposition.

Hosts: The only host previously recorded is the buprestid *Chrysobothris femorata* (Oliv.) (Brimley, 1942; Muesebeck and Walkley, 1951). However, in the U. S. National Museum are long series of *Spathius floridanus* from several hardwoods, reared under numerous Hopkins numbers which often list hosts and associated borers. These may be summarized as follows: from oak (*Quercus* spp.) (Hopkins Nos. 1460c, 1421c, 3016c, 3730e, 11861k and 12858a), hosts include *Chrysobothris femorata* and the cerambycid *Xylotrechus colonus* F.; from hickory (*Hicoria* spp.) (Hopkins Nos. 1489f, 3447c, 3636e, 3651d and 10975c1), hosts include *Chrysobothris* sp. and the weevil *Magdalis olya* Hbst., with several additional associated borers listed under No. 3636e; from chestnut (*Castanea dentata*) (Hopkins Nos. 10277b & c, 10701a-k, 11352a1, and 11353), hosts include *C. femorata* and *X. colonus*; for black walnut (*Juglans nigra*) (Hopkins No. 3640a-j), hosts are not specified but several associated cerambycids and buprestids are listed; for wild cherry (*Prunus* sp.) (Hopkins No. 10737i), parasitic on *Chrysobothris* sp.; for bald cypress (*Taxodium distichum*) (Hopkins Nos. 1732c and 1640e), host is unknown. Several additional Hopkins numbers are represented, but not listed here as they give no host tree or insect data.

SPECIES INQUIRENDA

Spathius honestor Say, 1828, Contrib. Maclur. Lyc. Phila. 1: 78.

The holotype specimen of this species is no longer extant, and the original description is inadequate to associate it, hence this species cannot be placed. Ashmead (1893) apparently did not know it, as he omitted it from his key. No hosts are recorded for this species.

SUMMARY

The braconid genus Spathius, ectoparasitic upon wood-boring beetle larvae, is revised for North America. Keys to both sexes and complete descriptions for the 21 recognized species are provided. Lectotypes are designated for the following species: brachyurus Ashm., brunneus Ashm., claripennis Ashm., longipetiolatus Ashm., sequoiae Ashm. and simillimus Ashm. New synonymies are: S. dignus Muesebeck and Walkley under S. brachyurus Ashm.; S. californicus Ashm. and S. brunneri Viereck under S. sequoiae Ashm.; and S. claripennis Ashm. and S. tomici Ashm. under S. canadensis Ashm. Newly described Spathius species include: aphenges, benefactor, brevipalpus, calligaster, comes, elegans, evansi, impus, marshi, parvulus and stigmatus.

A revised list of all verified previous and new host records includes representatives from six coleopterous families in both deciduous and coniferous trees; analysis indicates that specificity tends to be more to host habitat than to host taxon. Evidence for multiple oviposition in a single host is reported for two species, S. brachyurus and S. floridanus.

Evolutionary trends in the genus are discussed, and aspects of the biology reviewed, with particular reference to the Nearctic forms. Possible phyletic relationships are considered and the status of the four described spathiine fossils is clarified.

The long association of the name Spathius canadensis with parasites reared from elm bark borers is shown to be erroneous; rather, the status of S. canadensis is redefined to be a species which typically attacks scolytids in various coniferous trees. Most elm-reared specimens will belong to the new species, S. benefactor.

LITERATURE CITED*

- Aldrich, J. M. 1921. The division of insects in the United States National Museum. *Smithson. Ann. Rep. for 1919*, pp. 367-379.
- Ashraf, M. and M. M. Berryman. 1969. Biology of *Scolytus ventralis* (Coleoptera: Scolytidae) attacking *Abies grandis* in northern Idaho. *Melandieria* 2: 1-23.
- Ashmead, W. H. (1888) 1889. Descriptions of new Braconidae in the collection of the U. S. National Museum. *Proc. U. S. natn. Mus.* 11: 611-671.
- _____. 1891. Descriptions of some new Canadian Braconidae. *Can. Ent.* 23: 1-7.
- _____. 1893. Descriptions of new braconids bred by Prof. A. D. Hopkins. *Can. Ent.* 25: 67-79.
- Ayyar, P. N. K. and P. S. Narayanaswami. 1940. On the biology of *Spathius vulnificus* Wilk., a possible effective parasite of *Pempheres affinis* in South India. *Indian J. Ent.* 2: 79-86.
- Balch, R. E. and J. S. Prebble. 1940. The bronze birch borer and its relation to the dying of birch in New Brunswick forests. *For. Chron.* 16: 179-201.
- Barter, G. W. 1957. Studies of the bronze birch borer, *Agrilus anxius* Gory, in New Brunswick. *Can. Ent.* 89: 12-36.
- Beal, J. A. and C. L. Massey. 1945. Bark beetles and ambrosia beetles (Coleoptera: Scolytidae): with special reference to species occurring in North Carolina. *Bull. Sch. For. Duke Univ.* 10: 1-178.
- Bedard, W. D. 1938. An annotated list of the insect fauna of Douglas fir (*Pseudotsuga mucronata* Rafinesque) in the northern Rocky Mountain region. *Can. Ent.* 70: 188-197.
- Beyr, J. 1961. Ein Beitrag zur Kenntnis der morphologischen Variabilität bei *Spathius exarator* L. *Verh. XI. Int. Kongr. Ent., Wien 1960* 1: 229-232.
- Blackman, M. W. and H. H. Stage. 1918. Notes on insects bred from the bark and wood of American larch - *Larix laricina* (DuRoi.) Koch. *Tech. Publs N.Y. St. Coll. For.* 18: 9-115.
- _____. 1924. On the succession of insects living in bark and wood of dying, dead and decaying hickory. *Tech. Publs N.Y. St. Coll. For.* 24: 3-269.
- Brimley, C. S. 1942. Supplement to Insects of North Carolina. N. C. Dep. Agric., Raleigh, 39 pp.
- Brues, C. T. 1910. The parasitic Hymenoptera of the Tertiary of Florissant, Colorado. *Bul. Mus. comp. Zool. Harv.* 54: 1-125.
- _____. 1927. Observations on wood-boring insects, their parasites and other associated insects. *Psyche* 34: 73-90.
- Bushing, R. W. 1965. A synoptic list of the parasites of Scolytidae (Coleoptera) in North America north of Mexico. *Can. Ent.* 97: 449-492.
- Bushing, R. W. and D. E. Bright. 1965. New records of hymenopterous parasites from California. Scolytidae (Coleoptera). *Can. Ent.* 97: 199-204.
- Cameron, P. 1905. On the phytophagous and parasitic Hymenoptera collected by Mr. E. Ernest Green in Ceylon. *Spolia zeylan.* 3: 67-97.
- Chamberlin, W. J. 1939. The bark and timber beetles of North America north of Mexico. *Ore. St. Coll. Coop. Assn., Corvallis.* 513 pp.
- Chittenden, F. H. 1897. The two-lined chestnut borer (*Agrilus bilineatus* Weber). *Circ. Bur. Ent. U. S. Dep. Agric. (ser. 2)* 24: 1-8.

*Abbreviations of periodicals follow World List of Scientific Periodicals, fourth edition, 1963.

- Clausen, C. P. 1940. Entomophagous Insects. McGraw-Hill, New York, 688 pp.
- Craighead, F. C. 1950. Insect enemies of eastern forests. Misc. Publs U.S. Dep. Agric. No. 657, 679 pp.
- Dalla Torre, C. G. 1898. Catalogus Hymenopterorum. 4. Braconidae. G. Engelmann, Leipzig, 323 pp.
- De Leon, D. 1952. Insects associated with Sequoia sempervirens and Sequoia gigantea in California. Pan-Pacif. Ent. 23: 75-91.
- Doane, R. W., E. C. Van Dyke, W. J. Chamberlin and H. E. Burke. 1936. Forest Insects. McGraw-Hill, New York, 463 pp.
- Doutt, R. L. 1959. The biology of parasitic Hymenoptera. A. Rev. Ent. 4: 161-182.
- Eady, R. D. 1968. Some illustrations of microsculpture in the Hymenoptera. Proc. R. ent. Soc. Lond. (A) 43: 66-72.
- Felt, E. P. 1906. Insects affecting park and woodland trees. Mem. N.Y. St. Mus. 8(2): 333-887.
- _____. 1915. 29th Report of the State Entomologist, 1913. Bull. N.Y. St. Mus. 175: 1-257.
- Fischer, M. 1966. Studien über Braconiden (Hymenoptera). Z. angew. Zool. 53: 215-234.
- Fiske, W. F. 1907. Notes on the insect enemies of wood boring Coleoptera. Proc. ent. Soc. Wash. 9: 23-27.
- Foerster, A. 1862. Synopsis der Familien und Gattungen der Braconen. Verh. naturh. Ver. preuss. Rheinl. 19: 225-288.
- Gahan, A. B. and S. A. Rohwer. 1917, 1918. Lectotypes of the species of Hymenoptera (except Apoidea) described by Abbe Provancher. Can. Ent. 49: 391-400; 50: 196-201.
- Godwin, P. A. and T. M. Odell. 1965. Life history of the white pine cone beetle, Conophthorus coniperda. Ann. ent. Soc. Am. 58: 213-219.
- Heatwole, H. & D. M. Davis. 1965. Ecology of three sympatric species of parasitic insects of the genus Megarhyssa (Hymenoptera: Ichneumonidae). Ecology 46: 140-150.
- Hetrick, L. A. 1940. Some factors in natural control of the southern pine beetle, Dendroctonus frontalis Zimm. J. econ. Ent. 33: 554-556.
- Hoffman, C. H. 1938. Notes on Leperisinus aculeatus (Say) and its parasites (Coleoptera: Scolytidae). J. econ. Ent. 31: 118-119.
- Hopkins, A. D. 1892. Some bred W. Virginia Braconidae. Insect Life 4: 256-259.
- _____. 1893a. Catalog of West Virginia Scolytidae and their enemies with list of trees and shrubs attacked. Bull. W. Va. agric. Exp. Stn. 31: 119-168.
- _____. 1893b. Catalogue of West Virginia forest and shade tree insects. Bull. W. Va. agric. Exp. Stn. 32: 171-251.
- _____. 1899. Report on investigations to determine the cause of unhealthy conditions of the spruce and pine from 1880-1893. Bull. W. Va. agric. Exp. Stn. 56: 197-461.
- Ishii, T. 1953. On the biology of Spathius fuscipennis Ashmead, a rice stem borer parasite, in the Philippine Islands. Oyo Dobuts. Zasshi 18: 95-102.
- Iwata, K. 1959. The comparative anatomy of the ovary in Hymenoptera. Part III. Braconidae (including Aphidiidae) with descriptions of ovarian eggs. Kontyu 27: 231-238.
- Kaston, B. J. 1937. Notes on hymenopterous parasites of elm insects in Connecticut. Bull. Conn. agric. Exp. Stn. 396: 351-361.

- _____. 1939. The native elm bark beetle Hylurgopinus rufipes (Eichhoff) in Connecticut. Bull. Conn. agric. Exp. Stn. 420: 1-39.
- Kaston, B. J. and W. B. Becker. 1936. Spathius canadensis Ashm., a parasite of Hylurgopinus rufipes (Eichh.). J. econ. Ent. 29: 807.
- Lyngnes, R. 1955. Zur Kenntnis der Biologie von Spathius exarator L. (Hym., Bracon.). Z. angew. Ent. 38: 73-81.
- _____. 1960. Shape and function of the ovipositor in the three Hymenopterous species: Ephialtes extensor Thoms. (Ichneumonidae), Spathius exarator L. (Braconidae), and Plutothrix coelius Walk. (Chalcidae). Norsk ent. Tidsskr. 11: 122-134.
- MacAloney, H. J. 1930. The white pine weevil (Pissodes strobi Peck) - its biology and control. Bull. N.Y. St. Coll. For. 3: 1-87.
- Marsh, P. M. 1963. A key to Nearctic subfamilies of the family Braconidae (Hymenoptera). Ann. ent. Soc. Am. 56: 522-527.
- _____. 1965. The Nearctic Doryctinae. I. A review of the subfamily with a taxonomic revision of the tribe Hecabolini (Hymenoptera: Braconidae). Ann. ent. Soc. Am. 58: 668-699.
- Matthews, R. W. and P. M. Marsh. 1969. On the status of Cresson's Stenophasmus species from Cuba (Hymenoptera: Braconidae: Doryctinae). Proc. ent. Soc. Wash. 71: 94-98.
- Muesebeck, C. F. W. 1928. Family Braconidae. pp. 895-920. In: Leonard, M. D., List of the insects of New York. Cornell Univ. agric. Exp. Stn. Mem. No. 101, 1100 pp.
- _____. 1967. Family Braconidae. pp. 27-60. In: Krombein, K. V. and B. D. Burks, Hymenoptera of America North of Mexico. Synoptic Catalog. Agriculture Monogr. No. 2, suppl. 2, 584 pp.
- Muesebeck, C. F. W. and L. M. Walkley. 1951. Family Braconidae. pp. 90-184. In: Muesebeck, C. F. W., K. V. Krombein and H. K. Townes, Hymenoptera of America North of Mexico. Synoptic Catalogue. Agriculture Monogr. No. 2, 1420 pp.
- Nash, R. W., E. J. Duda and N. H. Gray. 1951. Studies on extensive dying, regeneration, and management of birch. Bull. Me. Forest Serv. 15.
- Nees von Esenbeck, C. G. 1818. Appendix ad J. L. C. Gravenhorst conspectum generum et familiarum Ichneumonidum, genera et familiam Ichneumonidum adscitorum exhibens. Nova Acta Acad. Caesar. Leop. Carol. 9: 299-310.
- Nixon, G. E. J. 1943. A revision of the Spathiinae of the Old World (Hymenoptera, Braconidae). Trans. R. ent. Soc. Lond. 93: 173-456.
- Pechuman, L. L. 1937. An annotated list of insects found in the bark and wood of Ulmus americana L. in New York State. Bull. Brooklyn ent. Soc. 32: 8-21.
- Pierce, W. D. 1908. A list of parasites known to attack American Rhyncophora. J. econ. Ent. 1: 380-396.
- Provancher, L. 1880. Faune Canadienne: Les Insectes Hymenopteres. Naturaliste can. 12: 161-180.
- _____. 1886. Additions a la Faune Canadienne - Hymenopterologique. Naturaliste can. 16: 121-157.
- _____. 1888. Additions a la Faune Hymenopterologique. Supplement aux additions aux Hymenopteres. Naturaliste can. 18: 370-397.
- Riley, C. V. 1873. Fifth annual report on the noxious, beneficial and other insects of the State of Missouri. Regan & Carter, Jefferson City, Mo. 160 pp.

- Riley, C. V. and L. O. Howard. 1890. Some of the bred parasitic Hymenoptera in the National Collection. *Insect Life* 2: 348-353.
- Robert, A. 1951a. Notes biologiques sur les principaux insectes parasites des charançons de l'orme: Eubadizon magdali Cress., Spathius canadensis Ash. (Braconides), Trigonura tarsata D. T., Trigonura sp. (Chalcidides, Hymenopteres). *Annls ACFAS* 17: 138-142.
- _____. 1951b. Role respectif de chacune des especes parasites dans la reduction des charançons de l'orme. *Annls ACFAS* 17: 143-147.
- _____. (1960) 1961. Les hymenopteres parasites des charançons de l'orme et leur influence sur leurs hotes dans le Quebec. *Ann. ent. Soc. Queb.* 6: 122-143.
- Russo, C. V. 1938. Contributo alla conoscenza dei Coleotteri Scolitidi Fleotribo: Phloeotribus scarabaeoides (Bern.) Fauv. Parte seconda. Biografia, simbionti, danni e lotta. *Boll. Lab. Entomol. Agr. Portici* 2: 1-420.
- Say, T. 1828. Descriptions of new species of Hymenoptera of the U. S. *Maclurian Lyceum, Phila.* 1: 67-83.
- Schedl, K. E. 1932. Parasites reared from forest insects in 1929. *Can. Ent.* 64: 1-2.
- Scudder, S. H. 1890. The tertiary insects of North America. *Rep. U. S. geol. Surv.* 13: 1-734.
- Shenefelt, R. D. 1968. Braconidae described by l'Abbe Provancher. *Naturaliste can.* 95: 627-656.
- Smith, F. 1859. Catalogue of hymenopterous insects collected by Mr. A. R. Wallace at the islands of Aru and Key. *J. Linn. Soc.* 3: 132-178.
- Snodgrass, R. E. 1941. The male genitalia of Hymenoptera. *Smithson. misc. Collns* 99 (14), 86 pp.
- Statz, G. 1936. Ueber alte und neue fossile Hymenopterenfunde aus den tertiären Ablagerungen von Rott am Siebengebirge. *Decheniana* 93: 256-312.
- _____. 1938. Neue Funde parasitischer Hymenopteren aus dem Tertiär von Rott am Siebengebirge. *Decheniana* 98A: 71-154.
- Tobias, V. I. 1967. A review of the classification, phylogeny and evolution of the family Braconidae (Hymenoptera). *Ent. Obozr.* 46: 645-669. [translation in *Ent. Rev.*, Wash. 46: 387-399.]
- Townes, H. 1962. Host selection patterns in some Nearctic ichneumonids. *Verh. XI. Int. Kongr. Ent.*, Wien 1960 2: 738-741.
- Viereck, H. L. 1910. Hymenoptera. pp. 579-700. In: Smith, J. B., *The insects of New Jersey. A. Rep. New Jers. St. Mus.* (1909), 888 pp.
- _____. 1912. Contributions to our knowledge of bees and ichneumon-flies, including description of twenty-one new genera and fifty-seven new species of ichneumon-flies. *Proc. U. S. natn. Mus.* 42: 613-648.
- Walker, F. 1874. Descriptions of some Japanese Hymenoptera. *Cist. Ent.* 1: 301-310.

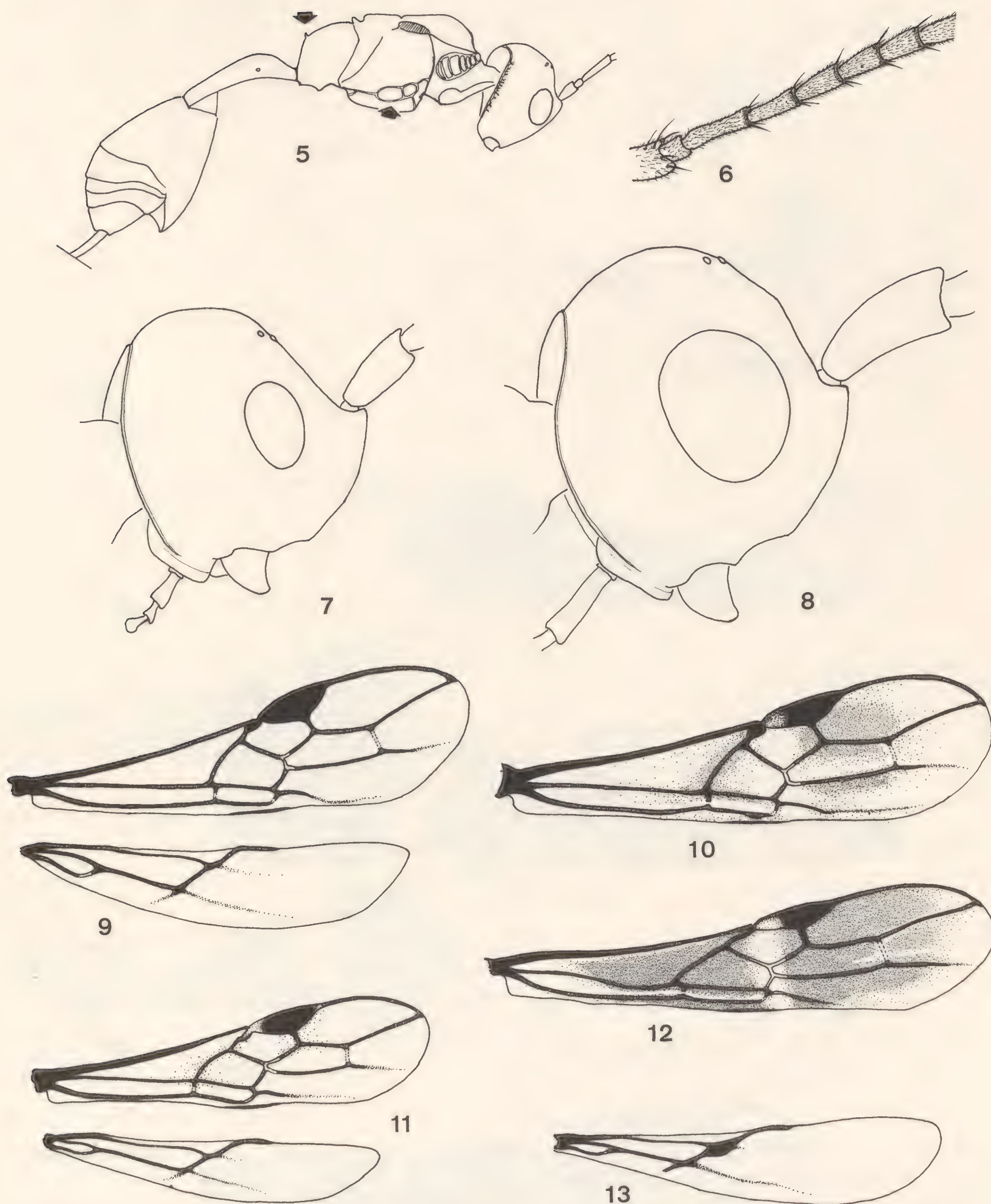


Figure 5. Spathius marshi, sp. n., lateral view of ♀; arrow above points to projecting carina separating areola and area petiolaris; other arrow points to sternaulus.

Figure 6. Portion of antenna of Spathius stigmatus, sp. n., showing basal flagellomeres, pedicel and apical part of scape.

Figure 7 and 8. Heads of Spathius brevipalpus, sp. n. and S. brachyurus Ashmead, respectively, lateral view, drawn at same magnification.

Figures 9 - 13. Wings of Spathius, all drawn at same magnification: 9. S. marshi, sp. n., ♀; 10. S. brachyurus Ashmead, ♀; 11. S. brevipalpus, sp. n., ♀; 12. S. stigmatus, sp. n., ♀; 13. S. stigmatus, sp. n., ♂ hind wing.

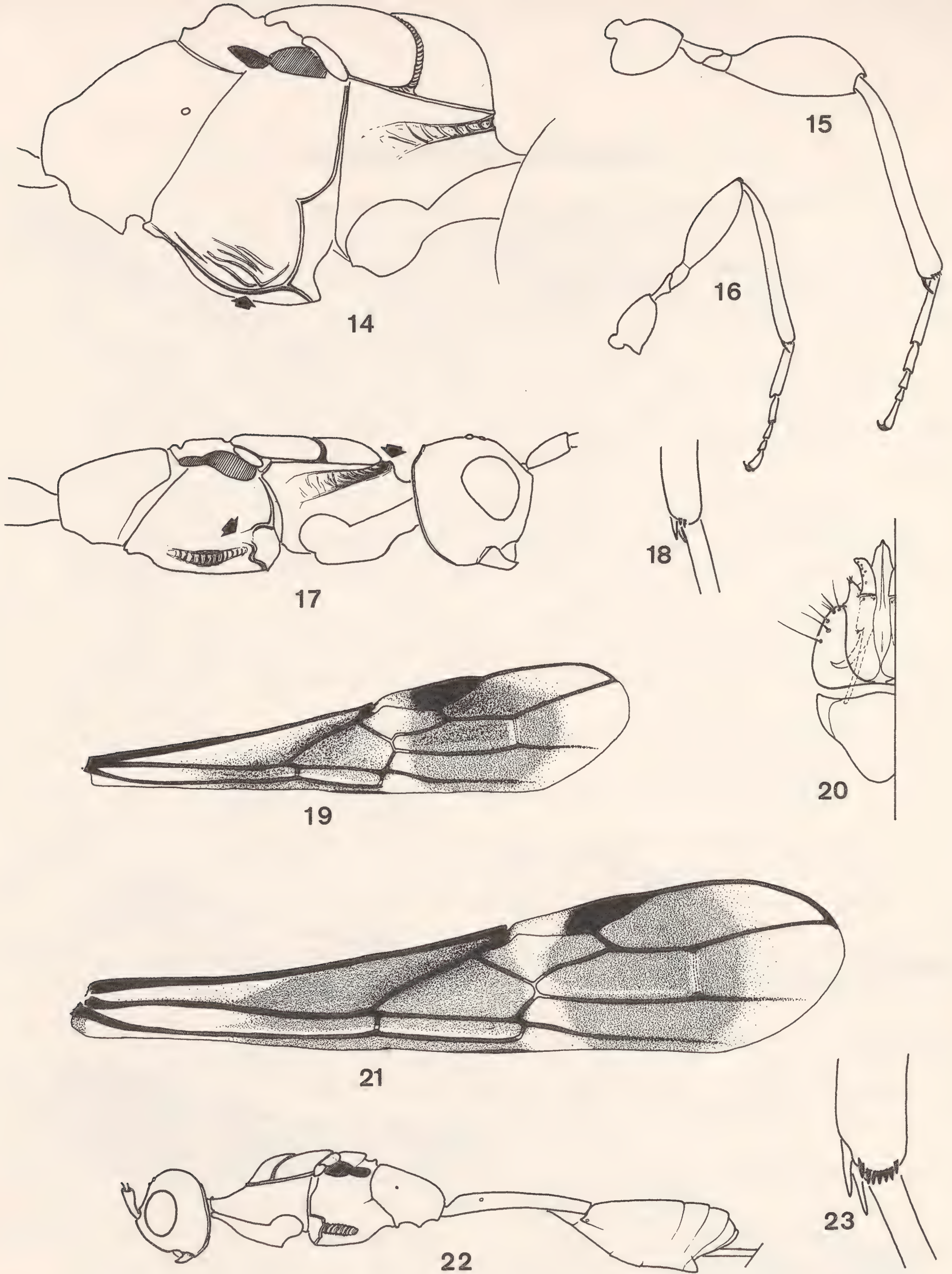


Figure 14. Thorax of Spathius brunneus Ashmead, lateral view; arrow points to longitudinal carina below sternaulus.

Figures 15 and 16. Hind legs of males of Spathius trifasciatus Riley and S. sequoiae Ashmead, respectively.

Figure 17. Head and thorax of Spathius calligaster, sp. n., lateral view, ♀; arrow above points to transverse swelling of prothorax, other arrow to incomplete prepectal carina.

Figure 18. Outer apical lobe of hind tibia of Spathius impus, sp. n.

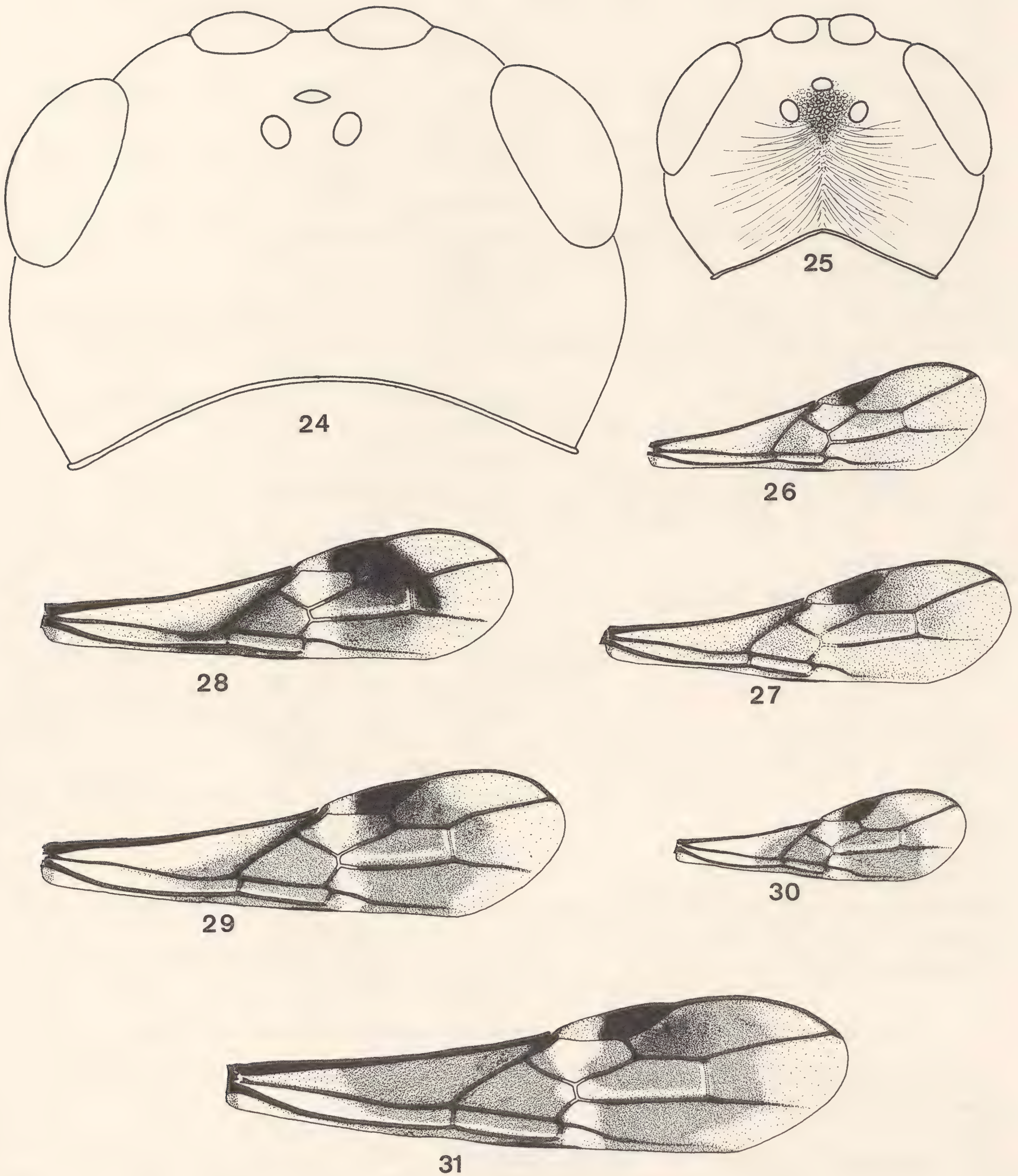
Figure 19. Fore wing of Spathius calligaster, sp. n., ♀.

Figure 20. Male genitalia of Spathius longipetiolatus Ashmead.

Figure 21. Fore wing of Spathius evansi, sp. n., ♀.

Figure 22. Spathius elegans, sp. n., lateral view of ♀.

Figure 23. Outer apical lobe of hind tibia of Spathius laflammei Provancher.



Figures 24 and 25. Heads of Spathius floridanus Ashmead and S. parvulus, sp. n., respectively; dorsal views at same magnification.

Figures 26 - 31. Fore wings of female Spathius, all drawn at same magnification:

26. S. aphenges, sp. n.; 27. S. sequoiae Ashmead; 28. S. pallidus Ashmead;
29. S. trifasciatus Riley; 30. S. parvulus, sp. n.; 31. S. comes, sp. n.

An asterisk indicates a synonym, misspelling, or nomen nudum.

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